Behavioural Studies of Free-Ranging Sharks: Direct Observation and Satellite Telemetry

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Abstract

Most elasmobranch species for which data are available have declined dramatically in recent years. Improved knowledge of the behaviour of sharks will help in designing conservation strategies and in improving public understanding and support for cartilaginous fishes. This thesis presents behavioural data from free-ranging sharks collected by direct underwater observation using videography and via satellite telemetry using pop-up satellite archival tags.

I describe for the first time voluntary stomach eversion in the Caribbean reef shark (*Carcharhinus perezi*) and jumping out of the water filmed from below the water surface for the blacktip shark (*Carcharhinus limbatus*). Both behaviours had been previously noted in different species but were rarely directly observed in free-living sharks. The direct observation of these behaviours enabled me to study their mechanics and discuss their ecological contexts.

Direct observation of free-ranging sharks allows for the study of interspecific associations. Certain shark species were found to be important hosts for echeneid fishes. I argue that the association between sharks and echeneids is best viewed as a subtle host – parasite interaction. Among the Echeneidae, the sharksucker (*Echeneis naucrates*) is known to attach to a wide variety of marine vertebrates, and I show for the first time that *E. naucrates* also attaches to conspecifics.

In the second section of this thesis, horizontal and vertical movement data collected with pop-up satellite archival tags are presented for the bull shark (*Carcharhinus leucas*) and the whale shark (*Rhincodon typus*). A total of 17 bull sharks were equipped with satellite tags in the Bahamas and Fiji and one whale shark in Mozambique. Both species spent most of their time in shallow water (bull sharks <50 m; whale shark <100 m) and, with the exception of the bull sharks tagged in the Bahamas (n = 6), they generally stayed deeper during the day than at night. For both shark species, I present the deepest dives ever directly recorded (204.4 m for the bull shark; 1285.7 m for the whale shark). The urgent need for international cooperation in devising conservation plans is underpinned by the fact that both species were found to cross national borders (Bahamas – United States of America for the bull shark; Mozambique – Madagascar for the whale shark). The introduction of satellite telemetry methods promises a deeper and previously unobtainable insight into marine vertebrate behaviour, movement patterns and ecological niches. Technical challenges such as premature releases still exist.

The kinds of behavioural data presented here will be useful for guiding conservation initiatives. As an example, I have applied my results to a small-scale conservation project in the South Pacific. In Fiji, the results are currently being used to set up and sustainably manage a small marine protected area called Shark Reef Marine Reserve.

Zusammenfassung

Die Populationsbestände vieler Hai- und Rochenarten haben in den vergangenen Jahren stark abgenommen. Daten über das Verhalten der Knorpelfische können helfen, nachhaltige Erhaltungsstrategien zu entwickeln und zu implementieren. Die vorliegende Arbeit präsentiert Verhaltensaspekte freilebender Haie, die durch direkte Unterwasserbeobachtungen (Videografie) und indirekt mit satellitengestützter Telemetrie gesammelt wurden.

Im ersten Teil der Arbeit beschreibe ich das aktive Magenausstülpen am Beispiel des Karibischen Riffhais (*Carcharhinus perezi*) und präsentiere eine mathematische Methode zur Berechnung der Wasseraustrittsgeschwindigkeit springender Schwarzspitzenhaie (*Carcharhinus limbatus*). Sowohl das Magenausstülpen wie auch das Sprungverhalten kennt man von verschiedenen Knorpelfischarten. Das Magenausstülpen konnte bei freilebenden Haien in ihrem natürlichen Lebensraum bislang nicht direkt beobachtet werden. Die direkte Beobachtung der beiden Verhaltensweisen erlaubt es, mechanische Aspekte derselben zu beschreiben und den ökologischen Kontext, in dem sie gezeigt werden, zu diskutieren.

Die direkte Beobachtung freilebender Haie erlaubt es, interspezifische Lebensgemeinschaften zu studieren. Viele Haiarten sind Wirte für Remoras (Echeneidae). Aus meinen Untersuchungen geht hervor, dass die Lebensgemeinschaft zwischen Haien und Remoras als Wirt-Parasit-Interaktion klassifiziert werden sollte. Innerhalb der Familie Echeneidae ist der Gestreifte Schiffshalter (*Echeneis naucrates*) dafür bekannt, viele marine Vertebraten als Wirte zu nutzen. Ich zeige zudem erstmals, dass *E. naucrates* sich auch an Artgenossen ansaugt.

Der zweite Teil der Arbeit analysiert Daten zu horizontalen und vertikalen Bewegungen von Bullen- (*Carcharhinus leucas*) und Walhai (*Rhincodon typus*). Die Daten wurden mit Hilfe sogenannter Pop-up Satellitensender gesammelt. Gesamthaft wurden 17 Bullenhaie in den Gewässern der Bahamas und der Fidschi-Inseln und ein Walhai vor Mosambik mit Satellitensendern ausgerüstet. Beide Arten hielten sich mehrheitlich in den obersten Wasserschichten auf (Bullenhaie <50 m; Walhai <100 m) und verbrachten – mit Ausnahme der Bullenhaie, die in den Bahamas beobachtet wurden (n = 6) – tagsüber im Vergleich zur Nacht mehr Zeit in tieferen Wasserschichten. Für beide Arten wurden die tiefsten je direkt gemessenen Tauchgänge (204.4 m für Bullenhaie; 1285.7 m für den Walhai) registriert. Dass die internationale Zusammenarbeit bei der Entwicklung und Implementierung von Schutzmassnahmen dringend notwendig ist, zeigt sich unter anderem daran, dass beide Arten nationale Grenzen durchschwammen (Bahamas – Vereinigte Staaten von Amerika für Bullenhaie; Mosambik – Madagaskar für den Walhai). Die Nutzung von Satellitentelemetrie verspricht tiefe und bislang nicht mögliche Einblicke in Verhaltensweisen, Bewegungsmuster und ökologische Nischen mariner Vertebraten. Noch nicht restlos gelöst sind aber diverse technische Aspekte (z.B. das frühzeitige Abfallen der Satellitensender).

Verhaltensdaten, wie sie in der vorliegenden Arbeit präsentiert werden, können der Implementierung von Schutzmassnahmen förderlich sein. Als Beispiel stelle ich ein lokales

Schutzprojekt im Südpazifik vor: Auf Fidschi wird gegenwärtig ein Teil meiner Daten dazu genutzt, einen kleinen Meerespark namens Shark Reef Marine Reserve aufzubauen und nachhaltig zu betreiben.

Part I

Introduction

Sharks at risk – urgent need for behavioural and ecological data

Much evidence suggests that large, long-lived marine vertebrates such as manatees, sea turtles, teleosts and sharks are declining precipitously due to overexploitation and habitat degradation (Jackson 2001; Myers & Worm 2003; Roman & Palumbi 2003; Stevens *et al*. 2005; Worm *et al*. 2005, 2006). Ocean ecosystems are influenced by changes in the physical environment, humans and especially fishery activities that affect more seriously species with high natural longevity and low reproductive rate (Botsford *et al*. 1997; Purvis *et al*. 2000). A major impediment to conservation at this stage is a lack of information about the basic biology of many species of concern, which stems in part from constraints in habitat accessibility and the logistical difficulty of monitoring large marine animals.

Anthropogenically-caused declines in animal population sizes can be addressed in different ways. Research into the different causes that lead to declines and how these causes affect different species can be used to develop species-specific management plans. At the same time, results from behavioural studies can be used to assist with management, to support the development of conservation efforts and to educate the lay public. Predators at the upper end of marine food chains integrate the dynamics of marine ecosystems across a wide range of spatial and temporal scales and offer new sources of information that can be used in setting management objectives. Maintaining top-predator populations is closely linked with maintaining a healthy ecosystem. For example, the creation of marine protected areas based upon the distribution of marine predators is a management procedure that has a wider-ranging effect upon ecosystem sustainability than procedures targeted at the exploited components of an ecosystem (Hooker 2006; Worm *et al*. 2006).

Sharks provide a good illustration of the general problem. Most species for which data are available have declined dramatically (Baum *et al*. 2003; Baum & Myers 2004; Casey & Myers 1998; Ward & Myers 2005). But there are widespread controversies over the status of pelagic fish stocks including sharks. For example, Myers & Worm (2003) argued that large pelagic fish stocks throughout the world were depleted to less than 10% of their original abundance by 1980. However, Hilborn *et al*. (2006) calculated that catches of this group of species have continued to rise for the last 25 years, and are much higher than they were during the period when they were supposedly being depleted. Furthermore, recent attempts to quantify rates of shark population decline have been criticized as overly pessimistic because of their reliance on trends recorded in logbooks (Burgess *et al*. 2005). Nevertheless, direct and

fisheries-independent observations have showed that rates of population declines are consistent with the hypothesis that elasmobranchs are suffering worldwide population reductions (Robbins *et al*. 2006).

Important international chondrichthyan conservation and management initiatives have commenced in the past decade, mainly focusing on the reduction of fishing pressure on populations (Fowler & Cavanagh 2005). These initiatives are of great importance not only for the conservation of elasmobranchs (sharks and rays), but also for a wide range of marine taxa and food webs (Bascompte *et al*. 2005; Mumby *et al*. 2006). Fisheries targeting sharks directly or indirectly are largely driven by the increasing global shark fin trade (Clark *et al*. 2006, 2006a), and therefore it is important to take into account economical considerations.

Chondrichthyan fishes (sharks, rays, and chimaeras) are among the most poorly known and least understood of all the major marine vertebrate groups. With the exception of a few commercially important species, for the majority of shark species basic biological key factors such as geographic distribution, reliable estimates of population size, life history, home range, movement and migration patterns, and trends in abundance are not available. This is the result of both the low priority placed on cartilaginous fish research and the considerable difficulty of data collection for many species.

A promising way to make progress in conservation of elasmobranchs is by studying their behaviour. To my knowledge, there are no examples in which shark populations have been protected as a direct result of behavioural research, but such work can contribute to placing conservation value on animals simply because behaviour has always been so fascinating to biologists and non-biologists alike. There are many areas in which the study of animal behaviour should provide a major contribution to solving conservation problems (Sutherland 1998). In some cases, for example, the behaviour itself is of interest and worthy of conservation. Motivation for studying animal behaviour can be, among others, the desire to preserve and maintain the environment or conserve and protect endangered species (Drickamer & Vessey 1992). The importance of conserving genetic variation and critical habitat is well accepted, but researchers should also consider the importance of conserving distinct behavioural patterns.

Attitudes towards elasmobranchs have changed in recent decades, and there is growing understanding of powerful incentives for sustainable recreational use of some elasmobranch resources (Anderson 2002). The use of such incentives as a conservation tool must be viewed as a positive opportunity, and will have its greatest impact when marine biologists are successful in explaining the biology and ecological importance of chondrichthyans, both from

a scientific perspective and to the non-researcher and lay public. A recent example is the worldwide media attention attracted by the report of an impressive round-trip transoceanic migration of a white shark (Bonfil *et al*. 2005). Such studies, while presenting valuable biological information to the scientific community, also attract public attention and can influence policy makers (e.g. the listing of the white shark on CITES Appendix II in 2004).

The study of shark behaviour and ecology

The main focus of the early papers calling for more shark behavioural research was their role as "dangerous and unpredictable predators" (Gruber & Myrberg 1977; Nelson 1977) and the aggressive behaviour of sharks towards humans was of primary concern (Myrberg 1976; Nelson 1981). Elasmobranchs, and especially sharks, are generally difficult to study in the wild and many logistical challenges still exist that hinder rapid advances. Due to these challenges, scientific understanding of shark behaviour has lagged far behind that of other taxa. Inherent challenges for studying shark behaviour and ecology include the size, longevity, and vagility of animals that live in a visually obscuring medium. In addition, some species, especially the larger ones, are considered dangerous to observe in the wild. Although few quantitative measurements of this danger exist (Johnson & Nelson 1973; Nelson *et al*. 1986), sharks, like any other predator, must be considered at least potentially dangerous.

In principle, sharks can be studied either in the wild or in a captive environment. While both approaches have advantages and disadvantages, studying shark behaviour under controlled conditions in a captive environment (e.g. Aronson *et al*. 1967; Crow *et al*. 1990; Henningsen 1994; Myrberg & Gruber 1974; Tester & Kato 1966) is limited because so few shark species can be successfully maintained in captivity (Dehart 2004; Smale *et al*. 2004). Furthermore, behaviour exhibited by captive animals may be muted or aberrant.

Observational studies on elasmobranchs in the wild can either be done on a three-dimensional scale (underwater) or on the water surface (e.g. from a boat or using a spotter plane). Sampling on the water surface can only be applied to species that regularly come to the water surface. These include the two plankton feeding species, the whale shark (Clark & Nelson 1997) and the basking shark (Hallacher 1977; Harvey-Clark *et al*. 1999), and the white shark (Bonfil *et al*. 2005).

The three-dimensional approach requires the observer to directly or indirectly enter the sharks' own environment. For centuries, many types of external and internal tags have been used on elasmobranchs for the purpose of identification and information retrieval (Kohler & Turner 2001). Various marking and tracking methods (e.g. conventional tagging, passive and

active acoustic tracking, satellite telemetry) have been applied to understand habitat use and preferences and movement patterns in sharks (Simpfendorfer & Heupel 2004; Voegeli *et al*. 2001). Technologies such as tracking animals by satellite have revolutionized the study of migrating marine animals in the past few years. It has improved basic knowledge of oceans, species, and key processes linking apex predators to their environments (Sims & Quayle 1998; Sims *et al*. 2000). Large shark species were among the first marine vertebrates to have been studied using satellite technology (Priede 1984). Today, state-of-the-art pop-up satellite archival tags (PSATs) are an invaluable tool for marine biologists to study the behaviour and ecology of large marine vertebrates (Block *et al*. 2005; Bonfil *et al*. 2005; Weng *et al*. 2005).

In conclusion, despite the remaining logistical challenges in shark behavioural research, recent technological advances are promising and the study of shark behaviour and ecology is a well established field in shark biology; many recent papers have highlighted the diversity of shark behaviour (e.g. Boustany *et al*. 2002; Braccini *et al*. 2005; Bush & Holland 2002; Cortés 2004; Heithaus 2004; Heupel *et al*. 2003, 2004; Pardini *et al*. 2001; Porcher 2005; Simpfendorfer *et al*. 2005; Sims 2003; Sims *et al*. 2006; Southall & Sims 2003; Wilson *et al*. 2001). Because new approaches have appeared only recently, many gaps in our knowledge of these fishes exist. For example, PSATs have only been used on large shark species that are commercially less exploited than many smaller ones. Also, archival satellite tags are of great value when studying species that show large-scale movement patterns but can also yield much needed information on the daily behaviour of less migratory species.

Today, the interest in the study of shark behaviour continues to increase rapidly, driven by the development of new technologies but also by the use of direct observational tools and techniques. While the use of satellite technology in shark research is limited in principle only by technical and logistical constraints, the direct observation of shark behaviour in the wild is often opportunistic and sample sizes are generally small. The overall challenge will be to overcome these difficulties and to provide decision makers with information on shark ecology and behaviour to produce conservation plans.

Objectives, structure, and research questions of this thesis

Following definitions by Lehner (1996), the research design of this study can be described as mensurative descriptive (Fig. 1) and the sampling method used as focal-animal sampling (Altmann 1974). Descriptive research, usually involving observations under natural conditions, can generate hypotheses which lead to experimental research (Bakeman & Gottman 1986). When studying taxa whose behaviour and ecology are largely unknown, it is

often necessary to use reconnaissance observations that help not only in formulating questions and defining objectives, but also in determining what aspects of behaviour can be measured, what manipulations are feasible, and the degree of variability that is to be expected (Lehner 1996). According to Marler (1975) this early stage in which the researcher becomes familiar with the animal's behaviour and ecology "is the most arduous and demanding aspect of behavioural study".

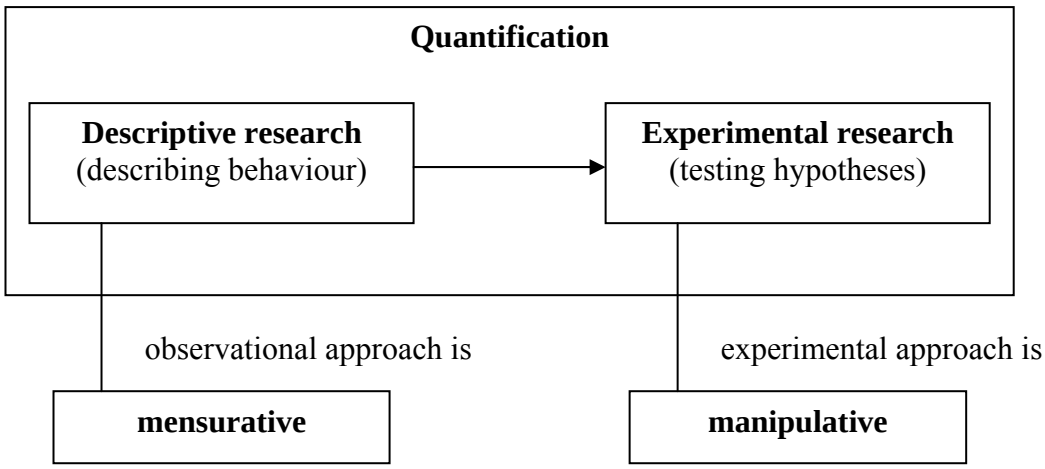

Fig. 1 Research design: description versus experimentation. Definitions follow Lehner (1996).

The thesis is divided into two sections. Section A presents behavioural and ecological aspects of the blacktip shark (*Carcharhinus limbatus*) and the Caribbean reef shark (*Carcharhinus perezi*) that were obtained by direct observational methods. As pointed out by Myrberg (1973), underwater videography can be a powerful tool for the marine biologist that provides scientists the opportunity not only to observe, directly, phenomena of interest, but also to collect data over sufficient periods of time so that quantitative analyses are possible (e.g. Brannan *et al*. 2003). Moreover, it has long been recognized that direct observations by divers can yield valuable information on the behaviour and ecology of elasmobranchs (Nelson 1977). Because underwater observations are made in the natural environment of the animal without any manipulation, behavioural observations are mainly anecdotal in nature. Nevertheless, the results can provide excellent preliminary data that benefit from follow-up studies using other methods or provide researchers with rare opportunities to witness complete and natural acts of, for example, mating (Whitney *et al*. 2004).

The first paper (A1) of this section demonstrates how studies using underwater videography as a tool can contribute to the understanding of a common association in the

marine realm, that between echeneids and their hosts. I provide some descriptive information on the interaction between free-ranging and captive sharks and sharksuckers (*Echeneis naucrates*) and ask the questions:

- Do sharks react to the presence of sharksuckers?
- Does sharksucker attachment cause an increase in shark swimming speed?

Most research presented in this paper was performed during my diploma thesis, and fits well within the scope of the PhD thesis. The second paper (A2) of this section presents the first report of the attachment of *Echeneis naucrates* to a conspecific and reviews the possible role of the relationship between echeneid fish and their hosts.

During data collection for the first paper of this section, I was able to observe and videotape two distinct behaviours in free-ranging Caribbean reef sharks and blacktip sharks, respectively. The third paper (A3) presented in this section looks at a unique behaviour in elasmobranchs that has never been documented before in a free-living shark: rapid voluntary stomach eversion. This novel observation allowed analysing the biomechanics and offers support for a "cleansing function" for stomach eversion. The fourth paper (A4) presents jumping blacktip sharks filmed from below the water surface and introduces a method to estimate the maximum swimming speed when penetrating the water surface.

Section B presents horizontal and vertical movement data from two shark species, the bull shark (*Carcharhinus leucas*) and the whale shark (*Rhincodon typus*), using satellite technology as an indirect observational tool. The introduction of satellite telemetry methods promises a deeper and previously unobtainable insight into marine vertebrate behaviour, movement patterns and ecological niches (Block *et al*. 1998, 2001, 2005; Bonfil *et al*. 2005; Boustany *et al*. 2002; Sims *et al*. 2003; Wilson *et al*. 2006), both by enabling us to track animals that otherwise would be difficult or impossible to observe, and also by providing indirect evidence of behaviour that occurs in our absence (Altmann & Altmann 2003).

The first paper (B1) in this section introduces Shark Reef Marine Reserve, Fiji, as a research site and reports a first, non-definitive fish species count with special emphasis on elasmobranchs. Within the elasmobranch fishes, special attention is given to the bull shark. The distribution of the bull shark in the South Pacific is little known (Brunnschweiler & Compagno 2007) and Shark Reef is among the few places in the region where bull sharks can be encountered in reasonable numbers year-round. However, the number of bull sharks seen at Shark Reef Marine Reserve decreases over the course of a calendar year, with few sightings

in the summer months. Comparable observations can be made in the Bahamas, where large bull sharks are frequently sighted in shallow coastal waters but move away during summer months. A likely explanation for the seasonal departure is that sharks travel to mating sites and nursery grounds.

Both Fiji and Walker's Cay in the Bahamas offer reliable and relatively easy access to free-ranging bull sharks. I attached PSATs to bull sharks at both locations before they left the tagging sites in late spring (September in the southern hemisphere and April in the northern hemisphere, respectively) in order to identify the ecological niche of the bull shark. Specifically, I asked the questions:

- Do bull sharks leave Fiji and/or Walker's Cay on large scale?
- Is it possible to find their mating sites and nursery grounds using PSATs?
- At what depths and temperatures can bull sharks be found?

Paper B2 describes a pilot study conducted in the Bahamas to test the use of PSATs to study bull sharks and paper B3 reports results from a total of 11 PSATs attached to bull sharks at Shark Reef Marine Reserve Fiji. These papers represent the first satellite tagging of bull sharks.

The fourth paper (B4) of this section describes the crossing of the Mozambique Channel by a whale shark. Mozambique has become a prime site for whale shark encounters in recent years. Preliminary results from photographic identification work suggest that the Tofo Beach area is an important feeding area for juvenile whale sharks, with a consistently high number of sightings year round (Simon Pierce, personal communication). Using PSATs I ask the question:

- Do whale sharks leave the Tofo Beach area on large scale?

Section B finishes up with two Appendixes: one that looks at some specific technical specifications and challenges involved with the use of PTT-100 pop-up satellite archival tags, and one summarises briefly the history of Shark Reef Marine Reserve.

All chapters and papers of this thesis were written by me. Contributions of varying degree have been made to the papers by the co-authors. The order of appearance is governed by the logic of content, not by chronology of paper submission or publication.

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Part II

Section A

Sharksucker–shark interaction in two carcharhinid species

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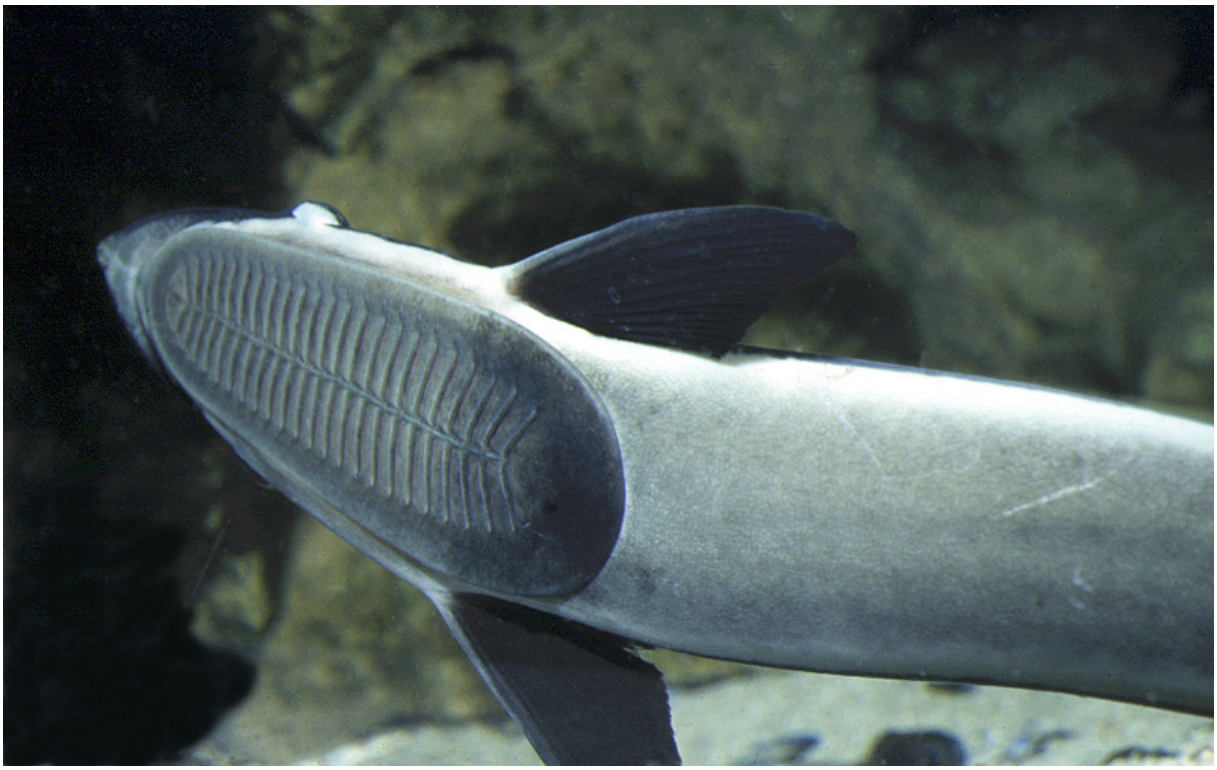

The unique suction disk of the remoras (Echeneidae) – a modified first dorsal fin that migrated anteriorly onto the neurocranium and underwent a series of morphological modifications – and its performance largely defines the interactions with their hosts. © Robert Patzner

ABSTRACT

It is not known whether sharksuckers have positive or negative effects on their hosts, partly because this association is difficult to study in free-ranging fish. I observed the behaviour of sharks with and without sharksuckers, to determine whether the hosts actively avoid sharksuckers. Wild blacktip sharks, *Carcharhinus limbatus*, took evasive actions when sharksuckers, *Echeneis naucrates*, attached to them, presumably to escape from skin irritation or hydrodynamical drag caused by the sharksuckers. Sharksuckers were most often attached to the belly or back of the shark, and sharks reacted most strongly to sharksuckers on their heads, sides, and dorsal fins. Observations of two captive bull sharks, *Carcharhinus leucas*, indicated that swimming speed increased when sharksuckers were attached. This paper supports the hypothesis that sharksucker attachment irritates sharks, and that the relationship between the two is best viewed as a subtle host–parasite interaction.

INTRODUCTION

Associations between different vertebrate classes are better known in terrestrial than marine animals (Dale 1992, Mooring & Mundy 1996). Even the well known example of a marine interspecific association, that between sharksuckers and their hosts, has not been well defined (Strasburg 1959, 1964, Cressey & Lachner 1970, Alling 1985, O'Toole 2002). Our lack of understanding arises from the difficulty in observing these interactions in free-ranging animals under natural conditions. Consequently, the costs and benefits for sharksuckers and their hosts are unknown and difficult to measure. One approach is to use the behaviour of the two organisms as a reflection of whether the association is beneficial or detrimental.

Sharksuckers, *Echeneis naucrates*, actively follow and attach to sharks by using their modified first dorsal fin (O'Toole 2002), so sharks seem obviously beneficial for sharksuckers (Cressey & Lachner 1970). But sharksuckers may themselves have either positive or negative effects on sharks. For example, it has been suggested that sharksuckers help to clean parasites off sharks (Strasburg 1959), but at the same time sharks occasionally attempt to dislodge sharksuckers or reposition them (Ritter 2002, Ritter & Brunnschweiler 2003). These behaviours have been interpreted to mean that sharksuckers have some kind of negative influence on sharks (Ritter & Godknecht 2000). Ritter (2002) divided the responses of sharks into rotational and nonrotational categories (Table 1). Rotational behaviours were either simple (any rotation along one of the three body axes: longitudinal, vertical, or lateral) or complex (a repetition of simple behaviour patterns to opposite sides, to the same side repeatedly, or a combination of simple behaviours). Patterns that did not include any rotation

along one of the three axes were defined as nonrotational (e.g. a quick shaking movement of a fin).

Ritter (2002) suggested that some of these behaviours in *Carcharhinus limbatus* were triggered by the presence of sharksuckers, but his data were not collected to test that hypothesis. What is needed are comparisons of behaviour between sharks with and without sharksuckers attached.

In this study I use observations of both captive and free-ranging animals to judge the reactions of swimming sharks to sharksuckers. The data from captive sharks have the advantage of unrestricted opportunities for observation and unimpeded visibility, whereas the data from wild sharks better represent the sharksucker–shark association under natural conditions. Specifically, I test (i) whether free-ranging blacktip sharks reacted to the presence of sharksuckers, and (ii) if sharksucker attachment causes an increase in swimming speed in captive bull sharks. I further report sharksucker attachment positions on the body of a shark and discuss the dynamics of the sharksucker–shark interaction.

MATERIALS AND METHODS

Between April and October 2000 off Walker‘s Cay, Abaco Islands, Bahamas, 510 blacktip sharks, *Carcharhinus limbatus*, were videotaped for 20 seconds from underwater, independent of sharksucker attachment. Duplicate observations of individuals that could be recognized from external markings were excluded from the analysis. I classified sharks as having either no sharksucker or at least one attached, and I recorded whether or not each shark showed a reaction, as defined in Table 1 (Ritter 2002). The sharks had an estimated total length between 1.2 and 1.5 m. Sharksuckers were between 15 and 30 cm with few animals exceeding this length. Data for male and female sharks were pooled and where necessary a standard Bonferroni method was used, indicated by p’.

For each blacktip shark with one or two sharksuckers attached, the position of the echeneid fish was recorded at the beginning of the sequence. The body of the shark was divided into the following regions: head (including gills), back, belly, side, dorsal fin, caudal fin and pectoral fins. Sharks with attached sharksuckers that were moving and sharks with more than two sharksuckers were excluded from this analysis. Sample sizes for analyses of behaviour and sharksucker attachment position are not the same, because in some cases sharks could not be videotaped for 20 s while in other cases a sharksucker was moving around multiple body regions of the sharks.

I tested the possibility that sharksucker position affects the response of the shark by comparing behaviour among blacktip sharks with sharksuckers located on different body regions. This analysis included only sharks with one sharksucker. I also recorded whether the reaction succeeded in forcing the sharksucker to change its position on the shark's body.

I collected data on the interaction between captive bull sharks and sharksuckers on three days between 15 and 17 January 2003 in the Seaworld Aquarium, Durban, South Africa. The shark tank (13.7 m x 9.2 m x 3.1 m) holds three elasmobranch species: one female and one male bull shark (both 2 m), six sandtiger sharks, *Carcharias taurus*, and one green sawfish, *Pristis zijsron*. The elasmobranchs are fed daily with dead fish. Both bull sharks have lived in this tank since they were captured 15 years ago. Other species were introduced to or removed from the tank during that time. In addition to elasmobranchs the tank holds several bony fish species, including sharksuckers, *Echeneis naucrates*. During data collection, two large sharksuckers (70–80 cm long) attached occasionally to both shark species. When not attached to one of the two shark species they swam freely in the water column.

Each of the three mornings, between 7:30 and 9:00 h and before the aquarium was open to the public, observations were collected using a focal-animal, all-occurrences sampling technique (Lehner 1996). After the start of the sample period both bull sharks were observed for 1 h and their behaviour with and without sharksuckers attached was noted using definitions given in Table 1. Because it was not possible to always keep both animals clearly in view, I recorded only whether or not a reaction occurred and not specific reaction patterns. Priority was given to the bull shark that had sharksuckers attached. Recording stopped after 1 h regardless of whether sharksuckers were attached to one of the sharks. On day 3, recording was stopped after 58 min because a diver entered the tank for maintenance. I noted attachment bouts and total sharksucker attachment time, as well as positions of the sharksuckers on the shark's body. A sharksucker attachment bout was defined as physical contact between the sharksucker's disk and the shark's skin.

A Sony DCR-PC3E, PAL digital camera (24 pictures per second) was used to film the behaviour of the sharks on the first 2 days. The camera was positioned at a window and observed about 30% of the tank (Fig. 1). I used this footage to estimate swimming speeds of the two bull sharks with and without sharksuckers attached. Both bull sharks constantly circled the tank in a clockwise or anti-clockwise direction, swimming close to the walls. Sequences of bull sharks swimming in a straight line and at the same depth from one end of the video screen to the other were used by measuring the time difference in seconds from the point of snout tip entering to the point where the snout tip departed from the screen.

RESULTS

Figure 2 shows the number of blacktip sharks with and without sharksuckers that did or did not show a reaction. Sharks without sharksuckers were significantly less responsive than sharks with sharksuckers attached ($\chi^2 = 37.1$; df = 1; $p < 0.0001$). Of the 15 sharks that were classified as showing a reaction but without having a sharksucker attached, nine showed primarily pectoral fin *flickering*. Twice this behaviour was associated with a *wind* motion, twice with a *pitch* motion, and once with a *roll* motion. With the exception of one shark observed where a *pitch* motion was connected to a *yaw* motion, all others showed *pitch* motions only.

Sharks without sharksuckers were less responsive compared to sharks with one and two sharksuckers attached ($\chi^2 = 33.8$; df = 1; $p' < 0.0001$ and $\chi^2 = 31.3$; df = 1; $p' < 0.0001$, respectively). Blacktip sharks with one sharksucker attached reacted equally often compared to sharks with two sharksuckers attached ($\chi^2 = 1.2$; df = 1; $p' = 0.277$).

I analyzed sharksucker attachment position for 345 sequences showing blacktip sharks (122 males; 223 females) with one sharksucker attached (Fig. 3). The majority of sharksuckers (39%) were positioned in the belly region, the back (27%) or on the pectoral fins (21%). Female and male sharks did not differ with regard to sharksucker attachment position ($\chi^2 = 4.1$; df = 6; $p = 0.659$). The positions of sharksuckers on the sharks (33 males; 45 females) with two sharksuckers attached were similar. In most cases (29%) one sharksucker was attached to the belly and the other was attached to the back. Two sharksuckers attached to the same body region were observed less often than expected ($\chi^2 = 51.8$; df = 1; $p < 0.0001$). In five cases both sharksuckers attached to the belly and in only one case they attached to the pectoral fins.

The reaction frequencies of blacktip sharks varied depending on where the sharksuckers were attached: head = 78%, side = 65%, dorsal fin = 64%, pectoral fins = 64%, belly = 48%, back = 28% and caudal fin = 6% ($\chi^2 = 42.5$; df = 6; $p < 0.0001$). The success rate of the simple behaviours (Table 1) was 25% (*flickering* included) compared to 28% for complex reaction patterns ($\chi^2 = 0.15$; df = 1; $p = 0.7$)

I observed the behaviour of captive bull sharks with sharksuckers attached for a total of 178 minutes. Sharksucker attachment bouts ranged between 0.4 and 20.2 minutes for the male bull shark and 0.3 and 8.2 minutes for the female bull shark (Table 2). Except for two brief occasions, the two sharksuckers attached to the same shark individual simultaneously. Changing from one animal to the other was not as a response to a visible reaction by the shark. In five out of the 11 attachment bouts, the female shark showed none of the reactions

described in Table 1. With the exception of one bout (4.7 min), these were all attachment bouts shorter than the average attachment time of 2.5 minutes (0.45; 0.37; 0.32; 0.97 min). The male bull shark showed no behavioural response in only two out of 21 attachment bouts, which were also well below the average attachment time of 4.8 minutes (0.5 and 0.57 min).

Bull sharks without sharksuckers attached showed a reaction in two cases, both involving the male. In one case the shark performed a *flicker* with its pectoral fins and in the other case it showed a *roll/flicker* pattern.

There were major differences between male and female sharks in the attachment position of the sharksuckers. With the exception of one attachment bout, sharksuckers attached to the male bull shark always in the back region. One sharksucker usually attached with its sucker disk between the first and second dorsal fin and the second sharksucker swam close to it without attaching. During one attachment bout with the male shark, the two sharksuckers were attached in the same position as described below for the female bull shark. When attaching to the female bull shark, the two sharksuckers were found in the belly region.

I estimated swimming speed from 188 film sequences with and without sharksuckers attached. Bull sharks with sharksuckers attached swam faster than those without sharksuckers (no sharksuckers: n = 124, crossing time = 7.3 sec ± 1 SD; with sharksuckers: n = 64, crossing time = 6.6 sec ± 1.2 SD; $t = -4.34$, $p < 0.0001$). These values correspond to an estimated swimming speed of 0.62 and 0.69 ms^{-1}, respectively.

DISCUSSION

The results indicate that sharksuckers alter the behaviour of sharks in captivity and in nature. This conclusion is based on the observation that sharks with sharksuckers attached showed several behaviours that have been classified as sharksucker induced (Ritter 2002). Although many free-ranging blacktip sharks with sharksuckers showed no reaction within the 20 s they were observed, I suspect that most sharks react sooner or later to the presence of sharksuckers. The duration of my observations of wild sharks was restricted by methodological constraints, and is certainly too short to be certain of detecting reactions to sharksuckers. This is supported by the bull shark data. I often record no reaction to the presence of sharksuckers for sequences well below the average time. The challenge of filming wild sharks may also explain why a few blacktip sharks with no visible sharksuckers showed evasive reactions. It is possible that a sharksucker was present but out of sight in some of these cases. Although introduced as a tool for marine biologists a long time ago (Myrberg 1973), underwater television still has its limits when working with wild animals.

The position of the sharksucker on the body of the shark may be important for both organisms (Mooring & Mundy 1996, Koenig 1997, Weeks 1999). Free-ranging blacktip sharks and captive bull sharks showed major differences with regard to sharksucker attachment position. While in the bull shark the two sharksuckers always attached to the same body region (although to different regions in the male and female shark), sharksuckers attaching to blacktip sharks were more variable in their position (Fig. 3). The reason for this pattern is unclear. The blacktip data suggest that the position of the sharksucker is important for the shark, because reaction frequencies were highest when a sharksucker was attached to the head, side, dorsal fin and pectoral fins.

The data from the free-ranging and captive animals illustrate strong correlations between shark behaviour and the presence of sharksuckers. Correlations alone do not demonstrate that sharksuckers *cause* responses, and it remains possible that some other agent affects both the behaviour of the shark and the presence of sharksuckers. I find this possibility unlikely, partly because there are plausible mechanisms connecting sharksuckers with evasive actions by sharks. One mechanism by which sharksuckers irritate sharks may involve hydrodynamic interference. Additional drag may arise when the echeneid fish attaches to a body region where it affects the structure of the boundary layer (Vogel 1994). In the case of the shark–echeneid interaction special attention has to be given to interference drag (Tucker 1990). The presence of a sharksucker can increase the drag of a streamlined body by an amount greater than the drag of the isolated sharksucker (Vogel 1994). Hydrodynamical aspects of sharksucker attachment are also important when considering swimming speeds (Brunnschweiler 2005). My finding that bull sharks with sharksuckers attached swam faster supports previous observations that sharks with sharksuckers increase speed as a response to sharksucker irritation (Brunnschweiler 2001). Higher speed in turn increases drag (Vogel 2003). Another possible disadvantage of having a sharksucker attached is sensory irritation when the echeneid fish is attached to sensitive body areas such as the lateral line or the head. Furthermore, sucking disc chaffing can cause damage to the host (Schwartz 1977, 1992).

Both species of sharks reacted as if they were irritated by the presence of the sharksuckers. This contradicts previous studies suggesting that the relation between echeneid fishes and their larger hosts is an example of commensalism or even mutualism, with the shark benefiting from removal of parasites or necrotic tissue (Strasburg 1959, Alling 1985, O'Toole 2002). Few data on stomach contents are available for *Echeneis naucrates*, but Cressey & Lachner (1970) found parasitic copepods or isopods in only 14 out of 95 stomachs and concluded that parasites are not a major food item. Although unlikely, another benefit for

the shark might be the consumption of sharksuckers. To my knowledge there is no published observation of a shark consuming a sharksucker. Commensalism occurs when two organisms benefit from one another, although one may gain more than the other. In the shark–sharksucker association, *E. naucrates* gains free transportation, protection, and possibly access to food sources, while the shark may derive only a small or negligible benefit from occasional cleaning. Therefore, my results suggest that sharks and sharksuckers exemplify a subtle host–parasite interaction. Its costs and benefits remain un-quantified and open for future studies.

SUMMARY

Ritter (2002) described shark behaviours that seem intended to remove or reposition sharksuckers, but he did not determine whether these actions are induced by the presence of sharksuckers. My study directly implicates sharksuckers in triggering evasive movements. Wild blacktip sharks with sharksuckers attached performed the actions defined by Ritter (2002) more frequently than those without, and they responded most often when sharksuckers were attached to potentially sensitive regions of the body. I also found that captive bull sharks swam more rapidly when sharksuckers were attached to them. Plausible causes of disturbance for the sharks include hydrodynamic interference and sensory irritation. This study therefore suggests that sharksuckers are detrimental to sharks and that this system may represent a subtle host–parasite interaction.

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Table 1. Behaviours observed in blacktip and bull sharks. With the exception of *sharp turn*, definitions follow Ritter (2002).

type	behaviour	description
rotational/simple	*roll*	rotational pattern along the longitudinal axis (Johnson & Nelson 1973, Klimley & Nelson 1981, Ritter & Godknecht 2000)
	yaw	rotational pattern along the vertical axis (Hobson 1963, Myrberg & Gruber 1974, Klimley 1985)
	pitch	rotational pattern along the lateral axis (Myrberg *et al*. 1972, Johnson & Nelson 1973)
rotational/complex	*sharp turn*	a combination of a *roll*, *yaw* and *pitch* motion and the shark ends up in a vertical turning position resulting in a 180º turn
	wiggle	a minimum of at least two *roll* patterns either to both sides or to the same side repeatedly
	wind	a combination of a *roll* and a *yaw* motion (Myrberg & Gruber 1974)
nonrotational	*yawn*	mouth opening, and lifting of the snout
	flicker	a quick shaking movement of any fin other than the caudal fin. Usually observed in combination with other patterns (Keyes 1982)

Table 2. Attachment bouts and average attachment time of sharksuckers for the male and female bull shark.

	male	female
attachment bouts	21	11
average attachment time	4.8 min (± 5.2 SD)	2.5 min (± 2.8 SD)

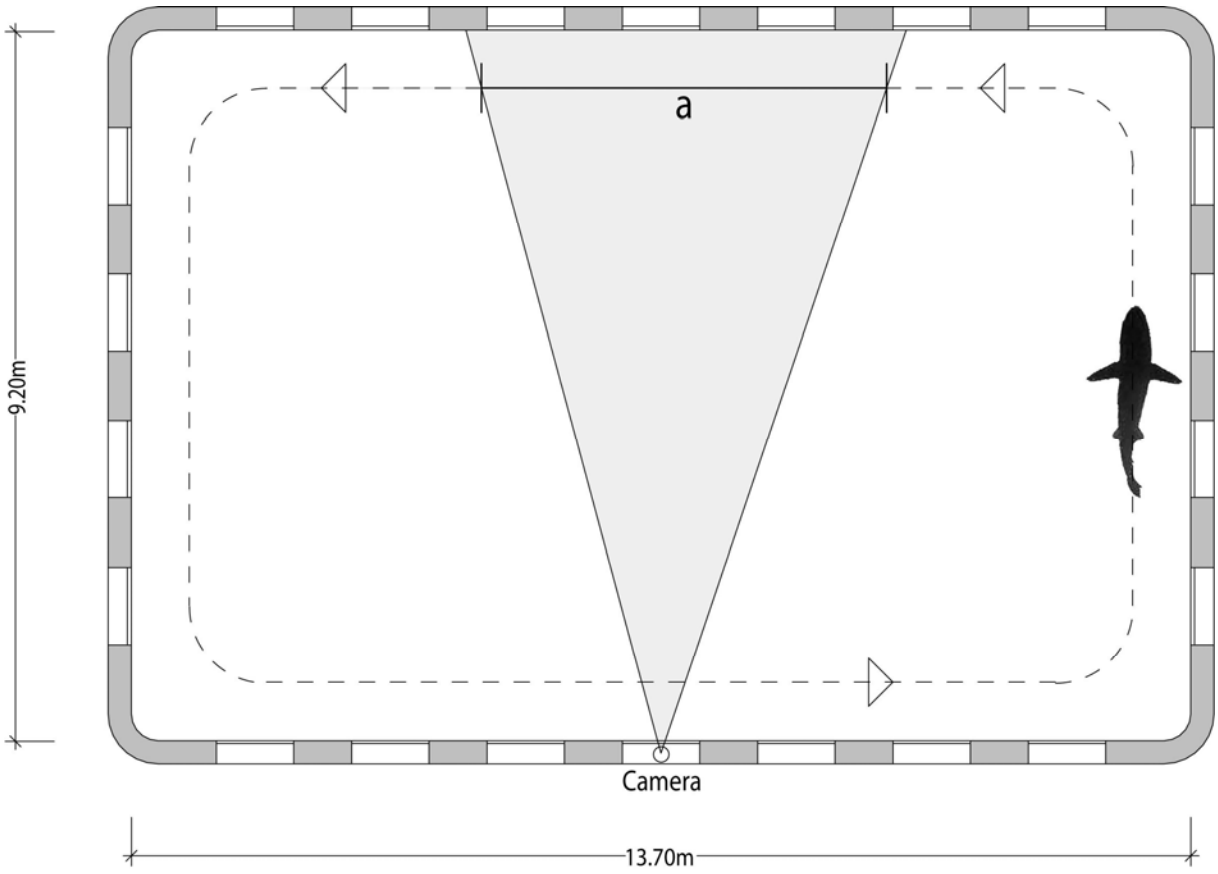

Figure 1. Durban Sea World shark tank. Dotted line with arrows shows a shark swimming in an anti-clockwise direction. The light grey shaded area was covered by the camera. 'a' indicates the distance used to measure swimming speed.

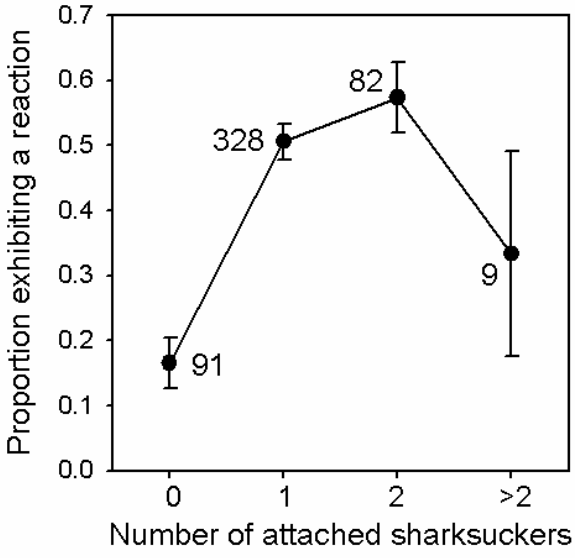

Figure 2. Proportion of wild blacktip sharks (n = 510) showing a behavioural response to different numbers of attached sharksuckers. Error bars show 1 SD.

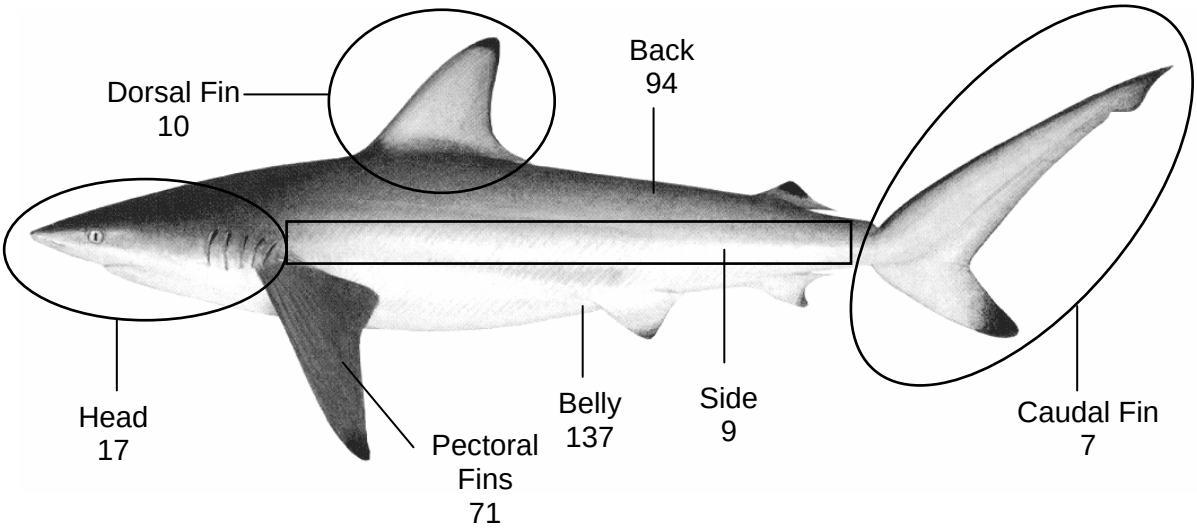

Figure 3. Distribution of sharksuckers on the body of blacktip sharks (n = 345) with one sharksucker attached.

A new and unexpected host for the sharksucker (*Echeneis naucrates*) with a brief review of the echeneid–host interactions

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The sharksucker (*Echeneis naucrates*) attaches to a wide variety of hosts including teleost fishes, elasmobranchs, marine turtles, and mammals. But also larger conspecifics serve as hosts from time to time. © Ron and Valerie Taylor

ABSTRACT

The sharksucker, *Echeneis naucrates*, attaches to a variety of hosts including teleost fish, elasmobranchs, marine turtles, and mammals. We list 18 additional hosts not previously recorded for this species, including the first report of its attachment to a conspecific and review the possible role of the relationship between echeneid fish and their hosts. The attachment of *E. naucrates* to a conspecific represents an addition to known hosts for this species, but it remains unclear if remoras are a habitual host for conspecifics.

The Echeneidae contains eight recognized species in four genera that all rely on hitchhiking behaviour to varying degrees (O'Toole, 2002). Among them, *Echeneis naucrates* (Linnaeus 1758) displays the most eclectic behaviour and is known to attach to a wide variety of hosts including teleost fish (Cressey & Lachner, 1970), marine mammals (Fertl & Landry, 1999; Williams et al., 2003), turtles (Sazima & Grossman, 2006), and sharks (Brunnschweiler, 2006). Whereas several teleost fish species serve as hosts for *E. naucrates* (reviewed in O'Toole, 2002), it has never been documented that echeneid fish also attach to conspecifics. Here we introduce *E. naucrates* as a new host for conspecifics, list 17 additional hosts for this remora species and review briefly the echeneid–host interactions.

Our record was made at the Shark Reef Marine Reserve, Fiji (for map and description see Brunnschweiler & Earle, 2006) on 20 March 2006. A group of eight medium-sized to large (30–50 cm total length, TL) *E. naucrates* was observed, including one individual which had a smaller conspecific attached to its back (Figure 1). The attached *E. naucrates* was a juvenile visually estimated to be approximately 10 cm TL (adults reach about 80–90 cm, see Randall, 1996; Humann, 2002). The two *E. naucrates* remained attached for at least two hours, and were video-taped for a total of 4:52 min.

The *E. naucrates* host individual was easily identified by its injured upper jaw (Figure 1). During the observation period, the smaller *E. naucrates* that was attached to its conspecific did not leave its host and was mostly attached to the same body region (dorsum). The host *E. naucrates* displayed movement patterns similar to those described for reef sharks when they presumably try to dislodge attached sharksuckers including shaking as well as shivering which included rolling and pectoral fin flickering (Brunnschweiler, 2006). These body movements had no apparent visible effect on the hitchhiking conspecific. The host sharksucker with injured upper jaw was not seen again at the study site the following days and thus it is unclear if the smaller conspecific stayed attached for longer than the observation period.

Juvenile *E. naucrates* (from hatching to approximately 60 mm standard length, SL, see Nakajima et al., 1987) are thought to live free-swimming and associate to floating objects (O'Toole, 2002). They start to attach to hosts at approximately 40–80 mm SL and are said to prefer boxfish (Ostraciidae) and parrotfish (Scaridae), these relatively small and sluggish hosts being regarded as trial vehicles (Strasburg, 1964). A porcupine fish (*Diodon hystrix* Linnaeus, 1758) recorded off Brazil (Figure 2) may possibly be regarded as a trial vehicle as well, as it carried a small *E. naucrates*. As the remoras grow they presumably switch to larger and/or faster hosts (Table 1; see review in O'Toole, 2002). Medium-sized to large sharksuckers are often recorded free-swimming (Strasburg, 1964; Sazima & Grossman, 2006; this paper) and it is likely that an adult *E. naucrates* would acquire a smaller conspecific under these particular circumstances, thus playing the role of a host.

At least 30 different fish serve as host species (some hosts unidentified to species level) for *E. naucrates* and it seems that no host is predominant (O'Toole, 2002). However, most host fish are reef-dwellers, a situation similar to that we recorded in Fiji, South Pacific and north-east Brazil, south-west Atlantic (Table 1), which is consistent with the reef-dwelling habits of *E. naucrates* (see O'Toole, 2002; Sazima & Grossman, 2006). Thus, about 50 fish species are recorded as hosts for *E. naucrates* to date. Unfortunately, for most of these records there is neither data on the size of the sharksucker nor the place of attachment to the host. On a stationary host *E. naucrates* is reported to move over the host's body and clean it (Sazima et al., 1999; Sazima & Grossman, 2006; our personal observations). Data on attachment location would be useful to test the hypothesis that small juvenile sharksuckers attach to a greater diversity of body parts than larger juveniles and adults (Silva-Jr & Sazima, 2006). For instance, the attachment of a small sharksucker on the head of a permit *Trachinotus falcatus* (Linnaeus, 1758) and a trunkfish *Lactophrys trigonus* (Linnaeus, 1758), contrasts with the predominant mode of attachment which primarily occurs on the hosts' ventral, dorsal or lateral surface (Table 1). Attaching to the head of a bottom feeding fish, such as the permit and trunkfish, allows the sharksucker to pick the food stirred up by the foraging host (our personal observation; see also Sazima & Grossman, 2006).

The unique suction disk of the remoras – a modified first dorsal fin that migrated anteriorly onto the neurocranium and underwent a series of morphological modifications – and its performance (Fulcher & Motta, 2006) would largely define the interactions with their hosts. However, the relation between a remora and its host seems to differ for each echeneid species (Strasburg, 1959; Alling, 1985; O'Toole, 2002). The suction disk allows hitch-hiking behaviour which benefits echeneids with reduced costs of transportation and expenditure of

energy (Strasburg, 1957; Steffensen & Lomholt, 1983; Alling, 1985), access to food resources (Strasburg, 1959; Sazima et al., 2003; Sazima & Grossman, 2006), protection from predators (Silva-Jr et al., 2005), and presumably increased mating opportunities (Silva-Jr & Sazima, 2003). But the suction disk performance has also effects on the hosts. These effects are by far less well studied and only recently has the question of costs and benefits for the hosts been considered (Brunnschweiler, 2006; Sazima & Grossman, 2006; Silva-Jr & Sazima, 2006). A possible benefit for the host is cleaning with removal of parasites and diseased or injured tissue (Cressey & Lachner, 1970; Sazima et al., 1999; Silva-Jr & Sazima, 2006). This benefit is likely outweighed by the potential costs for the host, however. While factual evidences and hypotheses about the nature of these costs exist (Brunnschweiler, 2006; Sazima & Grossman, 2006; Silva-Jr & Sazima, 2006), no quantitative data are available as yet. However, evidence is increasing that at least some host types such as sharks and dolphins are discomforted or even impaired with echeneid attachment or position on their body, and subsequently try to dislodge or relocate the remoras (Brunnschweiler, 2006; Fish et al., 2006; Silva-Jr & Sazima, 2006). This may explain the finding that remoras attach to many different body parts on larger hosts and seem to prefer the dorsal and ventral surface of their hosts (Table 1; Brunnschweiler, 2006). Due in part to the dislodging behaviour of the host, echeneid fish often change location. Remoras need a relatively flat surface to generate seal (Fulcher & Motta, 2006), so they tend to attach to areas of the host that provide a broad flat surface. Further studies of the echeneid–host association may aim at identifying and quantifying costs that would result from echeneid attachment to different host species.

ACKNOWLEDGEMENTS

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Table 1. Records of additional fish hosts for the sharksucker (*Echeneis naucrates*) from Fiji, South Pacific and north-east Brazil, south-west Atlantic. Host sizes (cm total length, TL, except for wingspan for the ray*) estimated against objects of known size; *E. naucrates* TL calculated from photographs on hosts or visually estimated against the host size; placement of *E. naucrates* on moving hosts. On ten host species *E. naucrates* were recorded regularly (N not counted). Order of families follows Nelson (1994); species in alphabetical order. A, Atlantic; P, Pacific.

Host species	Host size	*E. naucrates* size	Placement on host body	Area
GINGLYMOSTOMATIDAE				
Nebrius ferrugineus	250-300	20-40	Ventral, dorsal, lateral	P
CARCHARHINIDAE				
Carcharhinus amblyrhynchos	120-180	</>20	Ventral, dorsal	P
Carcharhinus melanopterus	80-120	~15	Ventral, dorsal, lateral	P
Carcharhinus perezi	160-200	20-40	Ventral, dorsal, lateral	A
Negaprion acutidens	180-200	20-40	Ventral, dorsal, lateral	P
MYLIOBATIDAE				
*Aetobatus narinari**	50-60	~15	Ventral	P
ECHENEIDAE				
Echeneis naucrates (N=1)	50	10	Dorsal	P
CARANGIDAE				
Caranx ignobilis	120-140	~15	Ventral, head	P
Trachinotus falcatus (N=1)	70	8	Head	A
SERRANIDAE				
Epinephelus lanceolatus	250	</>20	Ventral	P
Mycteroperca bonaci (N=2)	100-120	25-30	Lateral, Ventral	A
Variola louti (N=1)	60	~15	Dorsal	P
LABRIDAE				
Cheilinus undulatus	100	</> 20	Ventral	P
LUTJANIDAE				
Lutjanus bohar	40-70	~15	Ventral, lateral	P
Lutjanus jocu (N=1)	50	20	Ventral	A
SCARIDAE				
Scarus trispinosus (N=1)	60	15	Lateral	A
OSTRACIIDAE				
Lactophrys trigonus (N=2)	35-40	8, 30	Head, ventral	A
DIODONTIDAE				
Diodon hystrix (N=1)	38	6	Dorsal	A

Figure 1. An adult sharksucker (*Echeneis naucrates*) about 50 cm total length (TL) with a juvenile conspecific about 10 cm TL attached to its back. An injured upper jaw (circle) identified this particular sharksucker. Other fish are *Lutjanus bohar*, one *Caranx ignobilis*, and an additional adult sharksucker. From a video frame by Mike Neumann.

Figure 2. A juvenile sharksucker (*Echeneis naucrates*) 6 cm TL attached near the dorsal fin of a porcupine fish (*Diodon hystrix*) 38 cm TL. Photograph by Maurício Andrade.

Rapid voluntary stomach eversion in a free-living shark

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The ability of elasmobranchs to exhibit stomach eversion was suspected at least 300 years ago from reports of sharks being line-caught with stomachs protruding orally: bull shark (*Carcharhinus leucas*) with its everted stomach. © William Robbins

ABSTRACT

Video observation of oral gastric eversion in a free-living Caribbean reef shark (*Carcharhinus perezi*) shows voluntary gastric eversion followed by retraction not only occurs, but is extremely rapid (lasting ~0.3 s). Eversion may occur by stomach relaxation–oesophageal contraction coupled with increased abdominal pressures to enable prolapse, and retraction by a mechanism analogous to suction feeding. This behaviour provides a 'cleansing' function for removing indigestible food particles, parasites or mucus from the stomach lining. Sharks, and possibly other animals with similar gut morphologies, may use this technique to help maintain a healthy alimentary tract.

INTRODUCTION

Gastric eversion followed by recovery has been induced experimentally by administration of emetic (vomiting) agents in amphibians and batoid elasmobranchs (Hukuhara et al., 1973; Naitoh et al., 1989, 1991; Sims et al., 2000). It may serve to evacuate gastric contents and, hence, is functionally analogous to vomiting in mammals. However, in the batoid *Raja*, and by extrapolation, other elasmobranchs in which this occurs, it has been proposed that this is a more efficient strategy to cleanse the gastric mucosa by rinsing away small indigestible food particles, sloughed mucosa and mucus (Sims et al., 2000), which would not be cleared by the more usual gastric compression and bulk ejection mechanism involved in vomiting (Andrews & Young, 1993). However, spontaneous gastric eversion has not been observed, to our knowledge, in any free-living vertebrate in the natural environment. The absence of direct observation raises the possibility that this behaviour does not occur naturally and thus does not fulfil a cleansing function.

The ability of elasmobranchs such as sharks to exhibit stomach eversion was suspected at least 300 years ago from reports of sharks being line-caught with stomachs protruding orally (e.g. Labat, 1728 cited in Budker, 1971). Here we characterize for the first time spontaneous oral eversion of the stomach in a free-swimming Caribbean reef shark (*Carcharhinus perezi*) in its natural habitat. Based on these observations we propose a mechanism for gastric eversion, and from observations of scavenging fish following the shark, propose a function for this peculiar activity.

MATERIALS AND METHODS

An underwater video recording (SONY PC3 digital camera with Sealux housing recording at 24 frames s^{-1}; no artificial illumination) of the Caribbean reef shark (*Carcharhinus perezi*)

was taken at Walker's Cay, Bahamas (latitude 27.240°N, longitude 78.401°W) in an open coral reef area. More than 10 h of behaviour of different reef sharks were recorded over a few days during which a stomach eversion sequence was observed (between 1000 and 1100 h on 14 April 2003) only once in an adult female approximately 1.8 m total body length as it cruised slowly just above the sea bottom at a depth of 12 m.

A 4-s time period containing 96 frames was selected for quantitative analysis because the shark was in good lateral profile facilitating measurement of body movements. Frame-by-frame analysis of this sequence was undertaken to characterize different body movements and to determine the timing of particular activity patterns (Adobe Premiere v.6, Adobe Systems Inc., San Jose, CA, USA). Precise measurements of body movements were made from individual frames: body angle, pharyngeal depth, abdominal depth and mouth gape (Figure 1A).

RESULTS

Prior to beginning video-recording, the shark had been under observation for approximately 10 min and its swimming behaviour did not differ from conspecifics in this location. Because of the relatively brief period of video recording made prior to the eversion episodes, description of the external changes accompanying eversion are limited to approximately 1s prior to each episode; in both cases peri-eversion behaviour was similar. Two episodes of overt oral gastric eversion lasting ~0.28 and 0.40 s were observed 1.52 s apart during the 4-s time period selected for detailed analysis (Figure 1B).

Approximately 0.20 s before the first episode of gastric eversion the abdominal depth began to increase coincident with a decrease in pharyngeal depth and wide gaping of the mouth (Figure 1B). At this point the body was straight, but the head and body (caudal of the dorsal fin) began to ventroflex and this continued as the stomach was externalized, reaching a maximum while the stomach was still visible. The head assumed a noticeably convex 'bulging' outline which was sustained while the stomach was everted. Pharyngeal depth reached a nadir and abdominal depth a plateau while the stomach was everted. The stomach appeared while the mouth was still closing and was accompanied by opening of the gill slits. The stomach reached its maximum visibility 0.12 s after its appearance and remained at maximum exposure for a further 0.04 s, with retraction taking a further 0.12 s (Figure 1B). Retraction occurred while the mouth appeared closed around the stomach and when the gill slits were closed. Immediately after disappearance of the stomach the caudal body became convex over ~0.40 s and a cycle of mouth gaping and closure occurred, accompanied by

increased pharyngeal depth and body straightening. While this cycle of activity in the inter-ejection period was broadly similar to that during gastric eversion, it differed because the gill slits were closed.

Similar events characterized the second eversion, namely a decrease in pharyngeal depth, mouth closing after a gape, body straightening and caudal body concavity (Figure 1B). The stomach was expelled forcibly and progressively over a period of 0.12 s and appeared to 'balloon' as if inflated (Figure 2E). It remained maximally exposed for 0.16 s and was retracted over 0.12 s. Gill slit opening accompanied stomach eversion. Once again, retraction began while the mouth was still closed around the stomach, but gaping followed full retraction. The gill slits were closed during retraction and afterwards the abdominal depth decreased towards the value measured prior to the onset of eversion behaviour (Figure 1B).

It was not possible to see whether any particulate material was expelled from the stomach during eversion because video images were of insufficient resolution. However, the behaviour of accompanying fish suggests that particles were ejected. Prior to oral eversion a horse-eye jack (*Caranx latus*) swam parallel to the shark in a lateral position between the first and second dorsal fins (Figure 2). During ventroflexion, when the shark's snout visibly dropped towards the seabed, the jack rapidly moved away from the shark, before returning to the same position. Approximately 0.75 s later the shark's stomach was visible externally for the first time and the jack moved downwards and forward to just behind the shark's right pectoral fin (Figure 2B). The second episode of gastric eversion was followed 0.37 s later by the jack rapidly turning upwards toward the shark's midline, where it lunged forward (Figure 3). This jack then returned to its previous position. Five other jacks swam towards the shark immediately after the second eversion. The first and last individuals moved into the video frame some 0.54 and 1.62 s respectively, after the first jack began moving (Figure 3).

DISCUSSION

This analysis of a serendipitously recorded novel behaviour in a wild shark provides the first quantitative description of this behaviour although the results must be treated with some caution because of the unknown health status of the animal, the brief period of observation and the sub-optimal position of the shark during parts of the recording. However, there were no obvious indications that the animal was other than healthy although it is impossible to know if the behaviour was induced by some recently ingested material or is a spontaneous behaviour (see below). Despite these limitations based upon the video analysis and studies of

feeding and vomiting in carcharhiniform sharks we propose a mechanism for eversion which requires confirmation by more direct methods.

For the stomach to be externalized requires part of it to be everted, passed through the pectoral girdle to the pharynx and then the jaws. It is clear from the recording that this is a forceful act. It is unlikely that this could be achieved if the stomach was in a contracted state so we propose that the first step is relaxation of the cardiac (proximal) stomach mediated by the autonomic nervous system (Young, 1983; Jensen & Holmgren, 1994). The point at which the animal is at its straightest, but with the caudal body slightly concave, a few hundred milliseconds prior to eversion, may be the point at which the stomach passes through the pectoral girdle. The apposition of the mucus-coated oesophageal and gastric mucosae would facilitate oral passage. Assuming that this is correct, how then is the relaxed stomach propelled orally?

A sustained increase in abdominal depth was recorded which could be consistent with an increase in abdominal pressure driven by lateral muscle groups. Circumstantial evidence implicated abdominal muscle contraction in oral eversion of the stomach in rays (Sims et al., 2000) and abdominal muscle contraction has been implicated in oral eversion of the stomach in frogs and toads (Naitoh et al., 1991). In the second eversion episode it is clear the stomach balloons out of the mouth and is 'inflated' from inside, which must be due to abdominal contraction. The reduction in pharyngeal depth and opening of the proximal gills is not consistent with a lowering of pharyngeal pressure needed to 'suck' the stomach into the pharynx and mouth. It is important to note that the stomach disappears from view before the mouth begins to open and that retraction, which takes only 0.12 s, occurs when the head and caudal body are at maximum ventroflexion with the gill slits closed. The mechanism by which retraction is brought about is unclear but could be facilitated by induction of a swallow indicated by the wide gaping and elevation of the snout. The entire eversion sequence is similar in duration (0.28 s and 0.40 s) to bite duration (0.38 s) in this species (Motta, 2004).

There are two main observations that support a 'cleansing' function for gastric eversion in sharks. Firstly, horse-eye jack and bar jack (*Carangoides ruber*) routinely school around Caribbean reef sharks and the behaviour of the horse-eye jack we observed following the shark during stomach eversion was characteristic of scavenging behaviour shown by these bony fish. The fast, directed movement of the jack towards the shark's body when the stomach was protruded, followed by a characteristic feeding lunge indicates orientation to items assumed to be sloughed from the gastric surface during eversion. The movements

toward the shark by other jacks probably arose as a result of them detecting the first jack's movement.

Our second observation consistent with stomach eversion serving as a 'cleansing' mechanism was the gastric lining appeared to be retracted between the fleshy parts of the jaws between which the teeth are embedded although we recognize that the position of the animal was not optimal for observing the mouth. If this action occurs as we describe it could wipe away any residual mucosa or mucus not removed by the forward momentum of the stomach itself when everted, or by forward swimming. By comparison, the frog uses its forelimbs to wipe away material from the gastric surface of a prolapsed stomach (Naitoh & Wassersug, 1996). The trigger for this complex behaviour involving coordination between the gut, respiratory and locomotor systems remains to be identified but arguably differs from that which induces vomiting used to remove indigestible material in bulk from the stomach.

Our results show gastric eversion occurs in a free-living shark and, by extension, may be widespread among animals with gut morphologies facilitating this behaviour (i.e. short, wide oesophagus; relatively untethered, mobile gut). Moreover, its function may be related to removal of indigestible food particles and mucus from the inner surface. It is known that captive Carcharhinid sharks can externalize their lower intestine by cloacal protrusion (Crow et al., 1990). Therefore, sharks, and possibly rays, appear able to externalize the major proportion of their alimentary canal. We speculate that sharks keep healthy alimentary tracts partly due to this periodic process of maintenance but this proposal requires more detailed study of this elusive behaviour in free-living animals.

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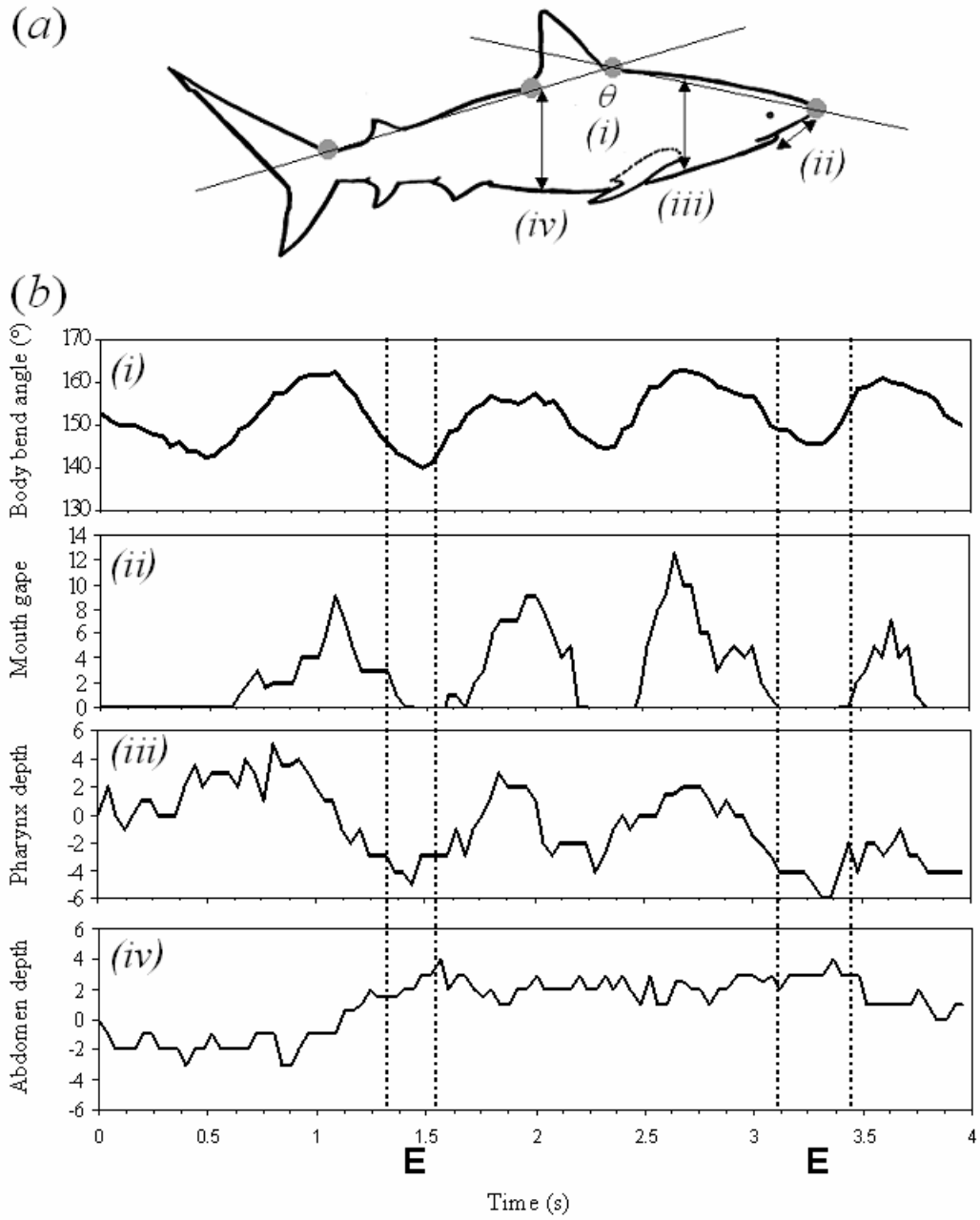

Figure 1. Body movement measurements (a) and dynamics (b) of a free-swimming *Carcharhinus perezi* during two episodes of gastric eversion (E). Body measurements *i-iv* in (a) correspond to changes in movements shown in (b) *i-iv*. The *y*-axis units in (b) *ii-iv* are arbitrary and denote relative changes in the body movements shown in (a).

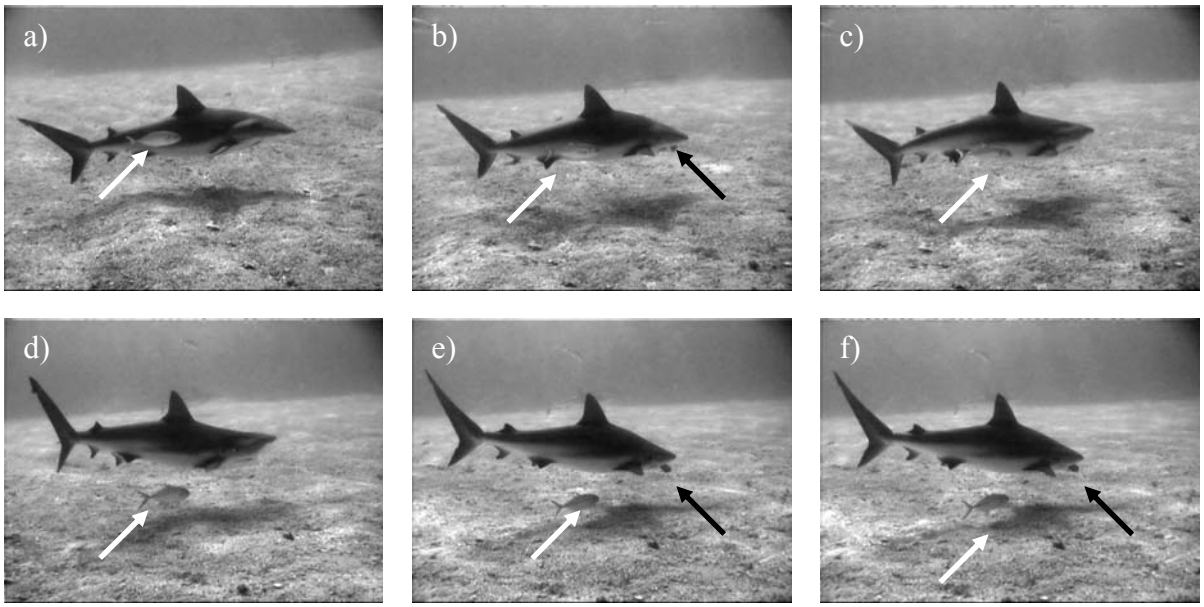

Figure 2. Episode 1 (a-c) and 2 (d-f) of oral gastric eversion. White arrows indicate position of the accompanying horse-eye jack (*Caranx latus*). Black arrows indicate the everted stomach.

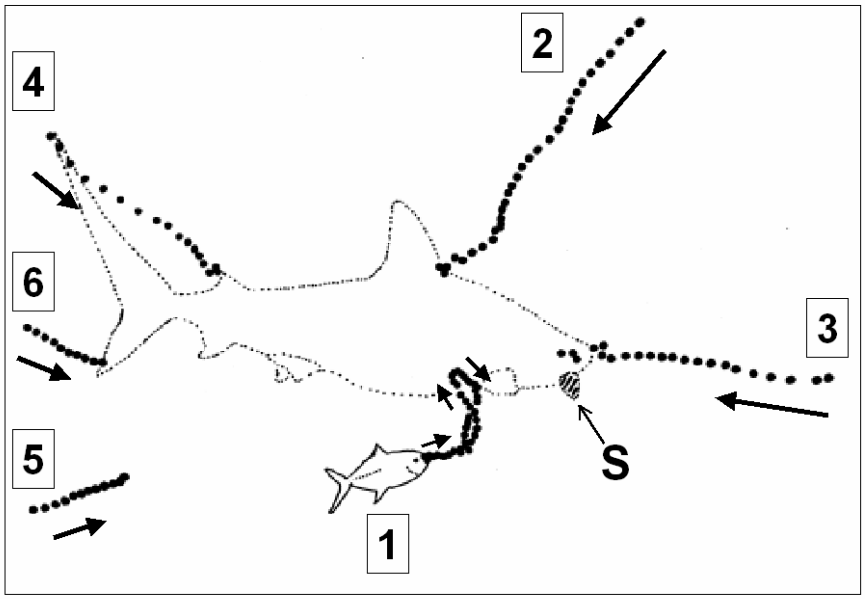

Figure 3. Behaviour and movements of six scavenging jacks (numbered 1-6) responding to gastric eversion (prolapsed stomach, S) in *Carcharhinus perezi*. Fish numbered in the order they responded to gastric eversion. Black dots represent successive positions of each fish's snout tip (0.04 s apart) over the entire sequence. Arrows give forward movement direction.

Water-escape velocities in jumping blacktip sharks

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A jumping white shark (*Carchardon carcharias*) – several shark species are known to regularly perform jumping behaviour; however, the mechanics and ecological context in which this spectacular behaviour occurs are poorly understood. © Klaus Jost

ABSTRACT

This paper describes the first determination of water-escape velocities in free-ranging sharks. Two approximations are used to estimate the final swimming speed at the moment of penetrating the water surface. Blacktip sharks were videotaped from below the surface and parameters were estimated by analysing the sequences frame by frame. Water-escape velocities averaged 6.3 ms^{-1}. These velocities for blacktip sharks seem accurate and are similar to estimates obtained for other shark species of similar size.

Swimming speed is important when considering the potential for active swimming behaviour to influence dispersal, energetics and metabolism. There are numerous methods for examining the swimming capabilities of fishes. Although difficult to obtain, undisturbed measurements of swimming speed have the advantage that speed is measured in the animal's natural environment.

Published estimates of the swimming speeds of sharks vary widely, in part due to differences in methodology (Carlson *et al*. 2004). In one experiment, free-ranging sharks were equipped with speedometers (Carey & Scharold 1990), while measurements were taken from animals swimming in a water tunnel in another (Graham *et al*. 1990). These methods cannot estimate maximum swimming speeds because the fishes cannot be induced to swim at a high speed (Webb & Keyes 1982) and the circumstances under which maximum swimming speeds occur are not known.

One opportunity for calculating a high swimming speed without manipulating the animal is by observing fishes jump from the water. This behaviour involves a 'standing jump', rather than porpoising, and probably requires a high level of burst swimming performance (Blake 1983). Many shark species jump and spin out of the water under certain circumstances (Compagno 1984, 2001). Members of at least two families (Lamnidae and Carcharhinidae) are known to jump with some regularity (Compagno 1984; Last & Stevens 1994; Anderson *et al*. 1996; Klimley *et al*. 1996). Few studies have addressed the ecological context in which jumps are performed (Castro 1996; Ritter & Brunnschweiler 2003). Detailed description of actual jumping behaviour is also lacking, mostly because of the difficulty of monitoring the behaviour of elasmobranchs in the open sea. Although other marine animals such as penguins and cetaceans are regularly seen performing jumping and porpoising behaviour (Jacobson 1986; Hui 1987), sharks are observed jumping and spinning only by chance. This makes it impossible to collect meaningful amounts of data. Consequently, a

detailed description of the swimming behaviour (swimming speed and body angle) of sharks under natural circumstances during vertical movements has not yet been produced.

Here, I develop formulae based on standard relationships in geometry and trigonometry for calculating water-escape velocity for a jumping shark. Two different approximations are used to estimate the final swimming speed at the moment of penetrating the water surface. The first approximation uses the conservation of energy equation:

$$E_h = \frac{1}{2}mv^2 + mgh, \tag{1}$$

where E_h is the energy needed at a given height (h), m is the animal's mass and v equals speed at any point during a projectile-like motion. At the water surface

$$E_0 = \frac{1}{2}mv_0{}^2. \tag{2}$$

Water-escape velocity can be expressed as $v = v_0\cos\alpha$, where v_0 is the speed while penetrating the water surface and α is the angle of the motion during the jump. E_h equals E_0 during any phase of the jump, which means that speed at the surface of the water can be expressed as

$$v_0 = \sqrt{\frac{2gh}{1-\cos^2\alpha}}. \tag{3}$$

The second approximation used to calculate speed (v_0) includes the duration (t) of the jump. With the shark projecting at an upward angle, the vertical component of the parabola is

$$y = v_y t - \frac{1}{2}gt^2. \tag{4}$$

Replacing v_y, it can be shown that

$$y = v_0 t\sin\alpha - \frac{1}{2}gt^2, \tag{5}$$

where y equals the height (h) of the jump and, hence,

$$v_0 = \frac{(h + \frac{1}{2}gt^2)}{t\sin\alpha}. \tag{6}$$

By analysing jump sequences of blacktip sharks (*Carcharhinus limbatus*) videotaped from below the surface, I estimated swimming speeds. Between April 2000 and November 2001, three blacktip sharks were filmed while performing jumps triggered by the presence of sharksuckers (Ritter & Brunnschweiler 2003). Jumping out of the water was observed only three times in more than 10 hours of behavioural observation, in each case involving adult females approximately 1.6 metres in total body length. I used two of these jumps to estimate final swimming speeds at the moment when the surface of the water was penetrated, but excluded the third because it was not possible to reliably estimate all parameters. The two jumping sharks were observed and filmed prior to accelerating towards the surface of the water for 45 seconds and 68 seconds, respectively. They were swimming horizontally at a constant cruising speed and started the acceleration to the surface from a depth of 10 m.

Two parameters, α and *t*, were measured by analysing the jumping sequences frame by frame (24 frames per second; table 1). The maximum height of the jump was estimated from the video by the extent to which the shark's body cleared the water. The equations used to calculate the errors are

$$\Delta v_0 = f'(h)\Delta h + f'(\alpha)\Delta\alpha = \frac{g}{\sin\alpha}\frac{1}{\sqrt{2gh}}\Delta h + \left|-\sqrt{2gh\frac{\cos\alpha}{\sin^2\alpha}}\right|\Delta\alpha, \qquad (7)$$

for equation (3) and

$$\begin{aligned}\Delta v_0 &= f'(h)\Delta h + f'(\alpha)\Delta\alpha + f'(t)\Delta t \\ &= \frac{1}{t\sin\alpha}\Delta h + \left|\frac{h+\frac{1}{2}gt^2}{t}\left(-\frac{\cos\alpha}{\sin^2\alpha}\right)\right|\Delta\alpha + \left|-\frac{h}{\sin\alpha}\frac{1}{t^2} + \frac{g}{2\sin\alpha}\right|\Delta t,\end{aligned} \qquad (8)$$

for equation (6). Parameters used for error calculation are $\Delta\alpha = \pi/36$, $\Delta h = 0.2$ m and $\Delta t = 1/24$ s for both jumps.

Both equations produce the same estimates of water-escape velocities for the two sharks (table 2). Swimming speed at the moment when the surface of the water was penetrated was about 6.3 ms^{-1}. This is higher than maximum speeds measured under laboratory conditions for makos (Graham *et al*. 1990) and other species (Carlson *et al.* 1999). In general, laboratory studies produce lower estimated swimming speeds than field studies (Block *et al.* 1992), presumably because jumping requires a very high burst speed and cannot easily be triggered under laboratory conditions.

The analysis used to estimate swimming speed is simple but requires simplifying assumptions. For example, the influence of drag was not considered. It is also assumed that the mass of the shark is concentrated in its centre of gravity. Therefore, the calculated speed is valid only if that point reaches height h. In reality, the shark's buoyancy contributes to propelling it from the water and this buoyancy decreases as the shark's body clears the water surface. The escape velocity of an animal performing a lower jump at a low angle will be most strongly affected when incorporating buoyancy: the value of g in equations (3) and (6) will decline and v_0 will be too high. One way to include buoyancy is to modify the numerator in equation (3) to $2g(h\text{-}h_1/2)$, where $h_1 = L/2\sin\alpha$ and L = body length of the shark. This results in $v_1 = 5.4$ ms^{-1} (-15%) and $v_2 = 4.9$ ms^{-1} (-23%; table 2).

Although both methods produce similar estimates of velocity for both sharks, there were considerable differences in the calculated error. For shark 2, the error was between 35% and 59% of the estimated speed (table 2). In comparison with shark 1, shark 2 jumped out of the water at a lower angle, reached a lower elevation and remained clear of the water for a shorter time. The error therefore increased when using the same parameters for error calculation as for shark 1.

Measuring swimming speeds in large free ranging fishes is difficult. Various methods have been applied in different species (Block *et al*. 1992; Nelson *et al.* 1997; Carlson *et al*. 2004). Variation also arises from differences in venue. For obvious reasons, fishes swim faster in the open ocean than in confined aquaria. Therefore, the method itself might be highly accurate, but the venue could strongly affect speed just because animals behave differently in different settings (Sims 2000). This variability makes comparison among species difficult. Furthermore, the method itself, for example, external speed sensing transmitters, can be problematic because additional drag might be induced, which lowers the overall performance of the animal (Sundström & Gruber 2002). Tag attachments can adversely affect fishes, biasing field data on their movement and behaviour (Mellas & Haynes 1985). It is therefore important to develop methods to estimate swimming speeds that do not include handling the fishes. The method proposed here offers the possibility of estimating speed by observing a jumping sequence occurring under natural conditions.

This paper adds an estimated swimming speed value for a shark species that has not previously been included in swimming speed measurement studies, and enlarges the dataset on estimated swimming speed in sharks. The calculated water-escape velocities for the two blacktip sharks seem accurate and are similar to estimates obtained for other shark species of similar size, for example, the lemon shark (*Negaprion brevirostris*; Sundström *et al*. 2001).

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Table 1. Parameter estimates used to calculate water-escape velocity for the two sharks (*h*, maximum height; *α*, angle of penetration; *t*, duration of jump)

parameter	shark 1	shark 2
h	1 m	0.5 m
α	45º	30º
t	0.438 s	0.375 s

Table 2. Estimated final swimming speeds (v_1, v_2) at the moment of penetrating the water surface for jumping sharks 1 and 2

equation	shark 1 (ms^{-1})	shark 2 (ms^{-1})
(3)	$v_1 = (6.3 \pm 1.2)$	$v_2 = (6.3 \pm 2.2)$
(6)	$v_1 = (6.3 \pm 1.2)$	$v_2 = (6.4 \pm 3.8)$

Section B

A contribution to marine life conservation efforts in the South Pacific: the Shark Reef Marine Reserve, Fiji

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Shark Reef Marine Reserve Fiji has excellent potential to become a prime site for long-term elasmobranch research. Up to eight different shark species can be encountered: a bull shark (*Carcharhinus leucas*) approaching a diver. © Sea Pics / Doug Perrine

ABSTRACT

We report a first fish species count for Shark Reef Marine Reserve (SRMR), Fiji, with special emphasis on elasmobranchs. In 2004, nine elasmobranch species were regularly observed at the site. The most common were *Carcharhinus leucas* and *Carcharhinus amblyrhynchos*. During a fish count in fall 2004 a total of 267 species of fishes were seen at SRMR, including members of 37 families, the largest being the Labridae. SRMR could serve as a model for local marine conservation efforts that can only be achieved by the creation of integrated management regimes which deal with all human activities and their effects.

INTRODUCTION

Large, long-lived vertebrates such as large fishes and sharks were the first to disappear from coastal ecosystems in response to human activities because of their life history characteristics and attention-attracting size (Jackson, 2001). Early population decline of large animals defines the first major transition in the history of coastal marine ecosystems. In many cases, the near-extirpation of large vertebrates preceded ecological investigations, so that their absence has been uncritically accepted as the natural "baseline" condition (Jackson, 1997). Reduced populations of larger fishes and habitat destruction have an immediate impact upon many economic and social activities because various uses of wildlife provide income, sustenance, or recreation for millions of people. It is therefore not surprising that interest in the conservation of biodiversity is increasing among the general public, as well as among behavioural ecologists who study wild animals and their environment.

One approach to marine conservation for particularly valuable sites involves the creation of small marine protected areas (MPAs), which try to accomplish ecological, economic, and social objectives such as recreation, education, and research (Bonfil, 1997). However, effective conservation of the marine environment can only be achieved by the creation of integrated management regimes which deal with all human activities and their effects, including both social objectives and fisheries management (Davis *et al*., 1997; Gell and Roberts, 2003). Biological recovery inside marine reserves appears to develop quickly, which facilitates the management of marine resources (Halpern and Warner, 2002).

Fulfilment of the various objectives of an MPA is difficult to measure. In most cases, baseline data (e.g. species diversity "before" and "after") are missing. Sites that are protected to some degree and used for recreation, education and research can be a promising way to foster non fishery-dependent marine conservation. However, such sites should be monitored closely because they have an immediate economic value (e.g. recreational divers want to

know what species they can expect to see). It is therefore important when implementing an MPA that a survey be done collecting baseline data for future comparison and development of the park.

This paper reports a first, non-definitive fish species count for Shark Reef Marine Reserve (SRMR) with special emphasis on elasmobranchs. Within the elasmobranch fishes, special attention is given to the bull shark, *Carcharhinus leucas* (Valenciennes in Müller and Henle, 1839), which is currently the Reserve's main attraction. SRMR is part of a small patch reef called Shark Reef (SR) on a fringing reef located off the southern coast of Viti Levu, Fiji (Fig. 1). In recent years SR has been used as a shark diving site by a local dive operator who, together with the Minister of Fisheries and Forestry and the local villages, which traditionally own the fishing rights on SR, established SRMR in April 2003.

MATERIALS AND METHODS

SRMR (S 18°18', E 178°01') is located on SR and covers approximately 300 m of the reef, encompassing an area that stretches to 300 m beyond the marker buoys. Since the official establishment of the Shark Reef Marine Reserve over the course of the year 2003, the local villagers are not allowed to fish in SRMR, but receive a "shark levy" of F$10 per diver per day in exchange. To attract large shark species, fish scraps are offered on a regular basis.

During 2003 an observer was trained to identify different shark species that visit SRMR. From January to December 2004, during each dive the observer noted the total number of individuals from all shark species present, as well as their sex whenever it could be determined. Dives always took place during the mornings (between 9 a.m. and noon) and to a maximum depth of 30 m. During 7 scuba dives between September 28 and October 1, 2004, a fish species count was conducted at SRMR by the second author to estimate fish diversity at the site. Depth for his census ranged from 3 m to 30 m. The purpose of this fish count was to provide divers visiting SRMR with a list of fishes they can expect to see there.

RESULTS

282 dives were conducted at SRMR during the year 2004. A total of eight shark species and one ray species were encountered at the site (Fig. 2): *Carcharhinus leucas*, *Negaprion acutidens* (Rüppell, 1837), *Galeocerdo cuvier* (Péron and Lesueur, 1822), *Carcharhinus albimarginatus* (Rüppell, 1837**)**, *Nebrius ferrugineus* (Lesson, 1831), *Carcharhinus amblyrhynchos* (Bleeker, 1856**)**, *Carcharhinus melanopterus* (Quoy and Gaimard, 1824), *Triaenodon obesus* (Rüppell, 1837), and *Aetobatus narinari* (Euphrasen, 1790). With the

exception of *G. cuvier*, all species were seen throughout the year, although some of them in low numbers. *G. cuvier* were not seen in the months of January, February, May, June, August, and September. The most abundant species at SRMR was *C. leucas*, followed by *C. amblyrhynchos*. The average number of *C. leucas* seen per month decreased over the course of the year, with the lowest numbers from October to December (Fig. 2). This was also the time of the year when the highest numbers of *C. amblyrhynchos* were recorded.

Table I presents the list of 267 species of fishes that were seen at SRMR during 7 fish survey dives by the second author. We have added *G. cuvier* and *A. narinari* to the list, both of which were observed at the site at other times during 2004. We also added *Manta birostris* (Walbaum, 1792) which has been observed by others at this site, but was not seen during the year 2004. The Labridae is the family represented by the greatest number of species, with a total of 45.

DISCUSSION

Determining where and how protected areas should be implemented is a complex issue that is of primary interest to conservation biologists, as protected areas will play a critical role in helping to protect biodiversity in the future (Deguise and Kerr, 2006). Economic importance is a criterion often used when deciding whether an area is to be designated as a MPA (Kelleher and Kenchington, 1992). In recent years an increasing number of recreational divers have visited SRMR, mainly because of its shark abundance. This is an obvious preliminary indication of the success of SRMR. However, our data provide no evidence as to how the local fish community has responded to the establishment of the marine park. To evaluate the ecosystem within SRMR, fish diversity will have to be quantified through time and habitat surveys will have to be conducted in conjunction with future fish surveys. Furthermore, to ascertain with confidence the influence of establishing and managing a protected area on the welfare of local people, it will be vital that conservation and social scientists conduct rigorous, controlled studies (Wilkie *et al*., 2006)

Fish species counts and fauna inventories can serve as a baseline for future studies that aim at estimating short- and long-term effects of MPA management decisions. The 267 species of fish (Tab. I) is a high species count for a few dives in a limited area for an island in the South Pacific. The abundance of fishes at SRMR may be the result of both the prohibition of fishing and the shark feeding itself, which provides many food scraps for other species. It is important to note that our approach overlooked inconspicuous species and did not yield quantitative estimates of relative abundance. Accordingly, the list has few species such as

gobies (only one of which is listed in table I), which would normally be the largest group in a survey for an area (Hawaii excepted) using standard methodology. This makes it difficult to meaningfully compare the SRMR osteichthyes fish list with lists from other areas using different methodology. Despite these constraints, the list can still contribute important information to the increasing marine conservation efforts in the region (Bazilchuk, 2006).

With the exception of *N. acutidens*, all elasmobranch species observed at SRMR in 2004 are confirmed for Fijian waters (Compagno, 1984; Last and Stevens, 1994). They all range at least to French Polynesia, although a single record of *C. leucas* from Rangiroa in the Tuamotu Archipelago reported by Johnson (1978) is undoubtedly a stray. *C. amblyrhynchos*, *C. melanopterus*, *G. cuvier*, *T. obesus*, and *A. narinari* range to the Pitcairn Islands (Randall, 1999). Of the sharks listed in table I, only *G. cuvier* occurs at Easter Island.

The number of *C. leucas* seen at SRMR is not constant, but decreases over the course of a calendar year, with most sightings in the first half of the year (Fig. 2). The pattern of a varying number of *C. leucas* present at a particular site can also be seen in other parts of the world, such as the Bahamas where most bull sharks leave the area in spring and early summer each year (Brunnschweiler and Van Buskirk, 2006). A likely explanation for a seasonal departure of *C. leucas* is that sharks move to mating sites and nursery grounds. Brunnschweiler and Van Buskirk (2006) confirmed a female bull shark swimming from Walker's Cay in the Bahamas into a known bull shark nursery (Snelson *et al*., 1984) on the Florida east coast within 12 days in spring. Currently, no nurseries or mating sites are known, and no quantitative data is available on the threat bull sharks are facing in Fijian waters and how closed areas would benefit this species. Thus, the ecological case for protection of an area can less often be based on concepts of critical habitat of endangered species or threat of extinction, it may more readily be based on protection of critical or important habitat for commercially or recreationally important species (Kelleher and Kenchington, 1992).

The establishment of SRMR is a first step to protect the fish fauna of a small reef patch off the southern coast of Viti Levu. This MPA, even if relatively small, could boost stocks outside the reserve sufficiently to benefit local fishermen and thus win their support. Under the guidance of a responsible dive operator, visitors to SRMR gain insight into how conditions might have been before human activity perturbated natural systems by removal of top level predators and unsustainable fisheries. The teaching of an ethical basis for respect of natural systems, which evolved over millions of years, but can be extinguished in several fishing seasons, may be the only viable long-term approach. The education to instill a conservation ethic can lead to the preservation of ecosystem values (Caddy and Seijo, 2005).

Arrangements that respect local claims and interests while also benefiting conservation goals are imperative.

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Randall J.E. (1999) Report on fish collections from the Pitcairn Islands. *Atoll Research Bulletin* 461: 1-36.

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Table I. Fishes seen during 7 scuba dives between September 28 and October 1, 2004 at Shark Reef, Beqa Lagoon, Fiji. Depth range 3 to 30 m. *Galeocerdo cuvier*, *Aetobatus narinari*, and *Manta birostris* were not seen during the fish survey but at other times in 2004 or before.

Family	Species
	Chondrichthyes
Carcharhinidae (requiem sharks)	
	Carcharhinus albimarginatus (Rüppell, 1837**)**
	Carcharhinus amblyrhynchos (Bleeker, 1856**)**
	Carcharhinus leucas (Valenciennes in Müller & Henle, 1839)
	Carcharhinus melanopterus (Quoy & Gaimard, 1824)
	Galeocerdo cuvier (Péron & Lesueur, 1822)
	Negaprion acutidens (Rüppell, 1837)
	Triaenodon obesus (Rüppell, 1837)
Ginglymostomatidae (nurse sharks)	
	Nebrius ferrugineus (Lesson, 1831)
Mobulidae (devilrays)	
	Manta birostris (Walbaum, 1792)
Myliobatidae (eagle rays)	
	Aetobatus narinari (Euphrasen, 1790)
	Osteichthyes
Acanthuridae (surgeonfishes)	
	Acanthurus blochii Valenciennes in C & V, 1835
	Acanthurus lineatus (Linnaeus, 1758)
	Acanthurus mata (Cuvier, 1829)
	Acanthurus nigricans (Linnaeus, 1758)
	Acanthurus nigricauda Duncker & Mohr, 1929
	Acanthurus nigrofuscus (Forsskål, 1775)
	Acanthurus nigrorus Valenciennes in C & V, 1835
	Acanthurus pyroferus Kittlitz, 1834
	Acanthurus thompsoni (Fowler, 1923)
	Acanthurus xanthopterus Valenciennes in C & V, 1835
	Ctenochaetus binotatus Randall, 1955
	Ctenochaetus cyanocheilus Randall & Clements, 2001
	Ctenochaetus striatus (Quoy & Gaimard, 1825)
	Naso brevirostris (Cuvier, 1829)
	Naso hexacanthus (Bleeker, 1855)
	Naso lituratus (Forster, 1801)
	Naso unicornis (Forsskål, 1775)
	Naso vlamingii (Valenciennes in C & V, 1835)
	Zebrasoma scopas (Cuvier, 1829)
	Zebrasoma veliferum (Bloch, 1795)

Apogonidae (cardinalfishes)

Ostorhinchus angustatus (Smith & Radcliffe, 1911)
Ostorhinchus cyanosoma (Bleeker, 1883)
Ostorhinchus nigrofasciatus (Lachner, 1953)
Pristiapogon kallopterus (Bleeker, 1856)

Aulostomidae (trumpetfishes)

Aulostomus chinensis (Linnaeus, 1766)

Balistidae (triggerfishes)

Balistapus undulatus (Park, 1797)
Balistoides conspicillum (Bloch & Schneider, 1801)
Balistoides viridescens (Bloch & Schneider, 1801)
Melichthys vidua (Solander in Richardson, 1845)
Odonus niger (Rüppell, 1836)
Rhinecanthus rectangulus (Bloch & Schneider, 1801)
Sufflamen bursa (Bloch & Schneider, 1801)

Blenniidae (blennies)

Cirripectes castaneus (Valenciennes in C & V, 1836)
Cirripectes variolosus (Valenciennes in C & V, 1836)
Escenius bicolor (Day, 1888)
Meiacanthus oualanensis (Günther, 1880)
Plagiotremus laudandus (Whitley, 1961)
Plagiotremus rhinorhynchos (Bleeker, 1852)

Caesionidae (fusiliers)

Caesio caerulaurea Lacepède, 1801
Caesio teres Seale, 1906
Pterocaesio marri Schultz in Schultz et al., 1953
Pterocaesio pisang (Bleeker, 1853)
Pterocaesio trilineata Carpenter, 1987

Caracanthidae (coral crouchers)

Caracanthus maculatus (Gray, 1831)

Carangidae (jacks)

Caranx ignobilis (Forsskål, 1775)
Caranx melampygus Cuvier in C & V, 1833
Caranx sexfasciatus Quoy & Gaimard, 1825
Elagatis bipinnulata (Quoy & Gaimard, 1825)
Gnathanodon speciosus (Forsskål, 1775)

Chaetontidae (butterflyfishes)

Chaetodon auriga Forsskål, 1775
Chaetodon baronessa Cuvier, 1829
Chaetodon bennetti Cuvier in C & V, 1831
Chaetodon citrinellus Cuvier in C & V, 1831
Chaetodon ephippium Cuvier in C & V, 1831
Chaetodon kleinii Bloch, 1790
Chaetodon lunulatus Quoy & Gaimard, 1825
Chaetodon mertensii Cuvier in C & V, 1831
Chaetodon pelewensis Kner, 1868
Chaetodon plebeius Cuvier in C & V, 1831
Chaetodon rafflesii Bennett, 1830
Chaetodon reticulatus Cuvier in C & V, 1831
Chaetodon ulietensis Cuvier in C & V, 1831
Chaetodon unimaculatus Bloch, 1787
Chaetodon vagabundus Linnaeus, 1758
Forcipiger flavissimus Jordan & McGregor in Jordan & Evermann, 1898
Forcipiger longirostris (Broussonet, 1782)

Hemitaurichthys polylepis (Bleeker, 1857)
Heniochus acuminatus (Linnaeus, 1758)
Heniochus chrysostomus Cuvier in C & V, 1831
Heniochus diphreutes Jordan, 1903
Heniochus singularis Smith & Radcliffe, 1911
Heniochus varius (Cuvier, 1829)

Cirrhitidae (hawkfishes)

Cirrhitichthys falco Randall, 1963
Neocirrhites armatus Castelnau, 1873
Paracirrhites arcatus (Cuvier in C & V, 1829)
Paracirrhites forsteri (Bloch & Schneider, 1801)
Paracirrhites hemistictus (Günther, 1874)

Echeneidae (remoras)

Echeneis naucrates Linnaeus, 1758
Remora remora (Linnaeus, 1758)

Fistulariidae (cornetfishes)

Fistularia commersonii Rüppell, 1838

Gobiidae (gobies)

Coryphopterus signipinnis (Hoese & Obika, 1988)

Haemulidae (sweetlips and grunts)

Plectorhinchus chaetodonoides Lacepède, 1801
Plectorhinchus picus (Cuvier in C & V, 1830)
Plectorhinchus vittatus (Linnaeus, 1758)

Holocentridae (soldierfishes and squirrelfishes)

Myripristis berndti Jordan & Evermann, 1903
Myripristis hexagona (Lacepède, 1802)
Myriprystis kuntee Valenciennes in C & V, 1831
Myripristis murdjan (Forsskål, 1775)
Myripristis pralinia Cuvier in C & V, 1829
Myripristis violacea Bleeker, 1851
Myripristis vittata Valenciennes in C & V, 1831
Neoniphon sammara (Forsskål, 1775)
Sargocentron caudimaculatum (Rüppell, 1838)
Sargocentron diadema (Lacepède, 1802)
Sargocentron microstoma (Günther, 1859)
Sargocentron spiniferum (Forsskål, 1775)
Sargocentron violaceum (Bleeker, 1853)

Kyphosidae (sea chubs)

Kyphosus cinerascens (Forsskål, 1775)

Labridae (wrasses)

Anampses caeruleopunctatus Rüppell, 1829
Anampses geographicus Valenciennes in C & V, 1840
Anampses neoguinaicus Bleeker, 1878
Anampses twistii Bleeker, 1856
Bodianus anthioides (Bennett, 1832)
Bodianus axillaris (Bennett, 1832)
Bodianus diana (Lacepède, 1801)
Bodianus loxozonus (Snyder, 1908)
Cheilinus chlorourus (Bloch, 1791)
Cheilinus fasciatus (Bloch, 1791)
Cheilinus trilobatus Lacepède, 1801
Cheilinus undulatus Rüppell, 1835
Cirrhilabrus exquisitus Smith, 1957
Cirrhilabrus punctatus Randall & Kuiter, 1989

Coris dorsomacula Fowler, 1908
Coris gaimard (Quoy & Gaimard, 1824)
Epibulus insidiator (Pallas, 1770)
Gomphosus varius Lacepède, 1801
Halichoeres biocellatus Schultz, 1960
Halichoeres hortulanus (Lacepède, 1801)
Halichoeres marginatus Rüppell, 1835
Halichoeres ornatissimus (Garrett, 1863)
Halichoeres prosopeion (Bleeker, 1853)
Hemigymnus fasciatus (Bloch, 1792)
Hemigymnus melapterus (Bloch, 1791)
Hologymnosus annulatus (Lacepède, 1801)
Hologymnosus doliatus (Lacepède, 1801)
Labroides bicolor Fowler & Bean, 1928
Labroides dimidiatus (Valenciennes in C & V, 1839)
Labropsis xanthonota Randall, 1981
Macropharyngodon meleagris (Valenciennes in C & V, 1839)
Oxycheilinus digrammus (Lacepède, 1801)
Oxycheilinus orientalis (Günther, 1862)
Pseudocheilinus evanidus Jordan & Evermann, 1903
Pseudocheilinus hexataenia (Bleeker, 1857)
Pseudocheilinus octotaenia Jenkins, 1901
Pseudodax moluccanus (Valenciennes in C & V, 1840)
Pteragogus cryptus Randall, 1981
Stethojulis bandanensis (Bleeker, 1851)
Thalassoma amblycephalum (Bleeker, 1856)
Thalassoma hardwicke (Bennett, 1830)
Thalassoma lunare (Linnaeus, 1758)
Thalassoma lutescens (Lay & Bennett, 1839)
Thalassoma nigrofasciatum Randall, 2003
Thalassoma quinquevittatum (Lay & Bennett, 1839)

Lethrinidae (emperors)

Lethrinus atkinsoni Seale, 1910
Lethrinus erythracanthus Valenciennes in C & V, 1830
Lethrinus olivaceus Valenciennes in C & V, 1830
Lethrinus xanthochilus Klunzinger, 1870
Monotaxis grandoculis (Forsskål, 1775)

Lutjanidae (snappers)

Aphareus furca (Lacepède, 1801)
Lutjanus bohar (Forsskål, 1775)
Lutjanus fulviflamma (Forsskål, 1775)
Lutjanus fulvus (Forster, 1801)
Lutjanus gibbus (Forsskål, 1775)
Lutjanus kasmira (Forsskål, 1775)
Lutjanus monostigma (Cuvier in C & V, 1828)
Lutjanus rivulatus (Cuvier in C & V, 1828)
Lutjanus semicinctus Quoy & Gaimard, 1824
Macolor niger (Forsskål, 1775)

Monacanthidae (filefishes)

Aluterus scriptus (Osbeck, 1765)
Cantherhines dumerilii (Hollard, 1854)

Mullidae (goatfishes)

Parupeneus barberinus (Lacepède, 1801)
Parupeneus crassilabris (Valenciennes in C & V, 1831)
Parupeneus cyclostomus (Lacepède, 1801)
Parupeneus multifasciatus (Quoy & Gaimard, 1825)
Parupeneus pleurostigma (Bennett, 1831)

Muraenidae (moray eels)

Gymnothorax flavimarginatus (Rüppell, 1830)
Gymnothorax javanicus (Bleeker, 1859)
Gymnothorax meleagris (Shaw, 1795)

Nemipteridae (breams and spinecheeks)

Scolopsis bilineatus (Bloch, 1793)

Ostraciidae (trunkfishes)

Ostracion cubicus Linnaeus, 1758
Ostracion meleagris Shaw, 1796

Pempheridae (sweepers)

Pempheris oualensis Cuvier in Lesson, 1831
Pempheris schwenkii Bleeker, 1855

Pinguipedidae (sandperches)

Parapercis clathrata Ogilby, 1911

Pomacanthidae (angelfishes)

Centropyge bicolor (Bloch, 1787)
Centropyge bispinosa (Günther, 1860)
Centropyge flavissima (Cuvier in C & V, 1831)
Genicanthus melanospilos (Bleeker, 1857)
Pomacanthus imperator (Bloch, 1787)
Pomacanthus semicirculatus (Cuvier in C & V, 1831)
Pygoplites diacanthus (Boddaert, 1772)

Pomacentridae (damselfishes)

Abudefduf sexfasciatus (Lacepède, 1801)
Abudefduf vaigiensis (Quoy & Gaimard, 1825)
Amblyglyphidodon aureus (Cuvier in C & V, 1830)
Amblyglyphidodon orbicularis (Hombron & Jacquinot, 1853)
Amphiprion chrysopterus Cuvier in C & V, 1830
Amphiprion clarkii (Bennett, 1830)
Amphiprion melanopus Bleeker, 1852
Amphiprion perideraion Bleeker, 1855
Chromis alpha Randall, 1988
Chromis amboinensis (Bleeker, 1873)
Chromis atripes Fowler & Bean, 1928
Chromis chrysura (Bliss, 1883)
Chromis delta Randall, 1988
Chromis iomelas Jordan & Seale, 1906
Chromis lepidolepis Bleeker, 1877
Chromis margaritifer Fowler, 1946
Chromis viridis (Cuvier in C & V, 1830)
Chromis weberi Fowler & Bean, 1928
Chromis xanthura (Bleeker, 1854)
Chrysiptera brownriggii (Bennett, 1828)
Chrysiptera rollandi (Whitley, 1961)
Chrysiptera taupou (Jordan & Seale, 1906)
Dascyllus reticulatus (Richardson, 1846)
Dascyllus trimaculatus (Rüppell, 1829)
Neopomacentris metallicus (Jordan & Seale, 1906)
Plectroglyphidodon dickii (Liénard, 1839)
Plectroglyphidodon johnstonianus Fowler & Ball, 1924
Plectroglyphididon lacrymatus (Quoy & Gaimard, 1825)
Pomacentrus brachialis Cuvier in C & V, 1830
Pomacentrus callainus Randall, 2002
Pomacentrus coelestis Jordan & Starks, 1901
Pomacentrus imitator (Whitley, 1964)
Pomacentrus nigromarginatus Allen, 1973

Pomacentrus spilotoceps Randall 2002
Pomacentrus vaiuli Jordan & Seale, 1906
Stegastes fasciolatus (Ogilby, 1889)

Ptereleotridae (dartfishes)

Nemateleotris magnifica Fowler, 1938
Ptereleotris evides (Jordan & Hubbs, 1925)

Scaridae (parrotfishes)

Cetoscarus ocellatus (Valenciennes in C & V, 1840)
Chlorurus bleekeri (de Beaufort in Weber & de Beaufort, 1940)
Chlorurus japanensis (Bloch, 1789)
Chlorurus microrhinos (Bleeker, 1854)
Chlorurus sordidus (Forsskål, 1775)
Hipposcarus longiceps (Valenciennes in C & V, 1840)
Scarus altipinnis (Steindachner, 1879)
Scarus chameleon Choat & Randall, 1986
Scarus frenatus Lacepède, 1802
Scarus ghobban Forsskål, 1775
Scarus niger Forsskål, 1775
Scarus psittacus Forsskål, 1775
Scarus rivulatus Valenciennes in C & V, 1840
Scarus rubroviolaceus Bleeker, 1847
Scarus schlegeli (Bleeker, 1861)
Scarus spinus (Kner, 1868)

Scorpaenidae (scorpionfishes)

Pterois volitans (Linnaeus, 1758)
Pterois radiata Cuvier in C & V, 1829

Serranidae (groupers and allies)

Anyperodon leucogrammicus (Valenciennes in C & V, 1828)
Belonoperca chabanaudi Fowler & Bean, 1930
Cephalopholis argus Bloch & Schneider, 1801
Cephalopholis leopardus (Lacepède, 1801)
Cephalopholis spiloparaea (Valenciennes in C & V, 1828)
Cephalopholis urodeta (Forster, 1801)
Epinephelus fuscoguttatus (Forsskål, 1775)
Epinephelus lanceolatus (Bloch, 1790)
Epinephelus macrospilos (Bleeker, 1855)
Epinephelus maculatus (Bloch, 1790)
Epinephelus polyphekadion (Bleeker, 1849)
Plectropomus leopardus (Lacepède, 1802)
Pseudanthias pascalus (Jordan & Tanaka, 1927)
Pseudanthias squamipinnis (Peters, 1855)
Serranocirrhitus latus Watanabe, 1949
Variola albimarginata Baissac, 1952
Variola louti (Forsskål, 1775)

Siganidae (rabbitfishes)

Siganus doliatus Cuvier, 1830
Siganus punctatus (Forster, 1801)
Siganus uspi Gawel & Woodland, 1974

Tetraodontidae (puffers)

Arothron mappa (Lesson, 1831)
Arothron nigropunctatus (Bloch & Schneider, 1801)

Zanclidae (moorish idols)

Zanclus cornutus (Linnaeus, 1758)

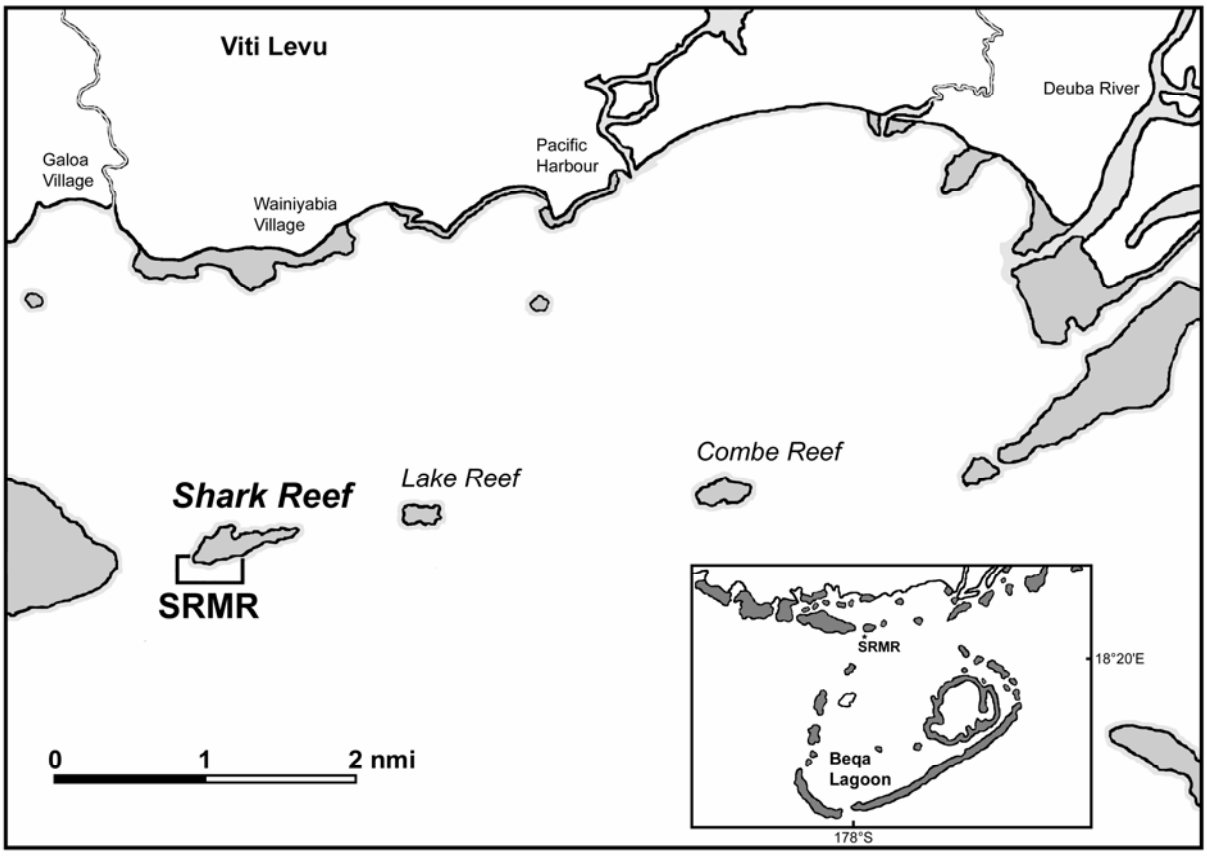

Figure 1. Location of Shark Reef Marine Reserve (SRMR) between Beqa Lagoon (inset) and the southern coast of Viti Levu. Dark grey areas indicate reef structures.

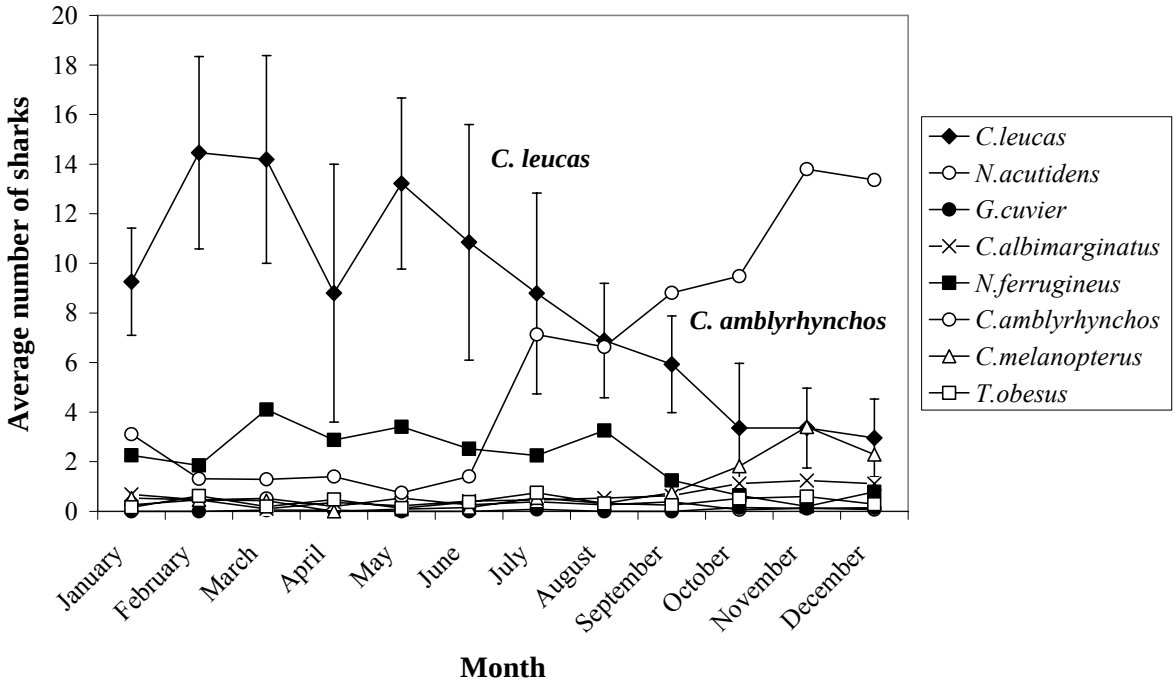

Figure 2. Average numbers of the different shark species per dive encountered each month at Shark Reef, Beqa Lagoon, Fiji, in 2004. For *C. leucas*, standard deviations are shown.

Satellite tagging of bull sharks at Walker's Cay in the Bahamas

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State-of-the-art pop-up satellite archival tags are powerful tools for marine biologists to understand migration and large-scale movement patterns of marine vertebrates and allow getting insight into habitat use: attaching a satellite tag onto a bull shark (*Carcharhinus leucas*) at Walker's Cay in the Bahamas. © Harald Baensch

ABSTRACT

Data on habitat use and movements are essential for designing conservation strategies, yet such data are rarely available for large marine animals such as sharks. This study reports the first satellite tagging of bull sharks, *Carcharhinus leucas*. Six bull sharks from the Bahamas were equipped with archival pop-up satellite tags to discover their movement patterns and depth and temperature preferences. The tags remained attached for 4 to 24 days and three sharks left the tagging site. One female moved within 12 days to a known nursery ground along the Florida coast. This is the first indication of movement of bull sharks between the Bahamas and the Florida coast, and it underscores the need for international cooperation in devising conservation plans

INTRODUCTION

Much evidence suggests that large, long-lived marine vertebrates such as manatees, sea turtles, teleosts and sharks are declining precipitously due to overexploitation and habitat degradation (Jackson, 2001; Myers and Worms, 2003; Roman and Palumbi, 2003). A major impediment to conservation at this stage is a lack of information about the basic biology of many species, which stems in part from the logistical difficulty of monitoring large migrating marine animals and accessing their habitats.

Sharks provide a good illustration of the general problem. Most species for which data are available have declined dramatically (Casey and Myers, 1998; Baum et al., 2003). Nevertheless, for the majority of shark species, basic information on geographic distribution, population size, and trends in abundance is not available. It is impossible to articulate conservation needs without knowledge about mating sites, nursery grounds, and migration routes to and from these areas. Considering life-history traits is crucial when forming goals or expectations for conservation strategies (Halpern and Warner, 2002).

Bull sharks have a worldwide distribution in coastal and freshwater habitats (Compagno, 1984) and large individuals are frequently sighted in shallow coastal waters. So far, no confirmed direct observations have been made of mating and pupping in coastal areas, and the sharks move away during the summer months (Brunnschweiler, pers. obs.). A likely explanation for the seasonal departure is that sharks travel to mating sites and nursery grounds. Nursery areas are discrete parts of the range where gravid females deliver young. Several bull shark nursery areas on the southeastern coast of the United States are known (Castro, 1993; Simpfendorfer et al., 2005; Snelson et al. 1984). However, the connections between specific populations and their nursery areas remain entirely unknown.

Bull sharks are often taken in fisheries throughout their range, although they are rarely a target species. Furthermore, their frequent occurrence in estuaries and freshwater makes them vulnerable to human impacts and habitat modification. As a consequence of their losses to fisheries and their habitat distribution, bull sharks are listed by IUCN as Near Threatened on a global scale (Cavanagh et al., 2003)

In this study we used archival pop-up satellite tags on bull sharks on Walker's Cay, Bahamas, to learn about their movement patterns and depth and temperature preferences. Pop-up satellite tags are a valuable tool for marine scientists studying pelagic fish movement (Block et al., 2005; Bonfil et al., 2005). This relatively new technology does not require recapture of the tagged sharks, and there is no need to return the tag to a tagging agency. Therefore, much information on movements and habitat preferences can be obtained from fewer tagged individuals (Sedberry and Loefer, 2001).

MATERIALS AND METHODS

Six bull sharks (two males, four females) were tagged on 8–9 April 2003 at Walker's Cay, Bahamas, with individually colour marked PTT–100 archival pop-up satellite tags (Microwave Telemetry, Columbia, MD). These tags archive hourly temperature and pressure readings and record time of sunrise and sunset for subsequent geolocation calculation. Tags are rated to withstand 3000psi (2000 m) and have an optional pressure initiated pop-off feature to allow the tag to pop off and start transmitting if it descends below a predetermined depth or remains at a constant depth over a predetermined length of time. After pop-up, data are transmitted through the Argos satellite system. Our tags had preset attachment intervals of 30 days (two tags), 60 days (two tags) and 90 days (two tags). Sex of the animals was determined from the presence of elongated claspers in males, and total length of the animals was estimated to be 1.8–2.5 m. Males mature at 1.6–2.3 m and females 1.8–2.3 m (Compagno, 1984).

To minimize stress, we deployed tags without catching the animals. Sharks were attracted with food to a platform built partly over the water and the tag was driven into the dorsal musculature below the first dorsal fin using a fiberglass spear. The full tag setup consisted of the pop-up satellite tag unit, a monofilament line marked with an individually coloured plastic tube, and a double barbed stainless steel anchor. Tagging was not severely stressful, because all tagged sharks immediately returned to feeding at the site. On the days following attachment, we checked the site where the sharks normally aggregate to see if tagged animals had remained in the area.

RESULTS

The tags remained attached to the sharks for 4 to 24 days, and during this time three animals left Walker's Cay while the other three stayed in the waters around the island (Fig. 1). All six tags detached prior to the programmed pop-up date, because the animals remained at a constant depth for four consecutive days and the pressure initiated pop-off feature was therefore activated. Bull sharks that did not leave the area (male #40597, female #40600, female #40601) had tags on for 24, 23, and 4 days, respectively. Those that moved away (female #40598, male #40599, female #40602) were tagged for 12, 12, and 4 days, respectively.

Depth and temperature data, recorded at one-hour intervals, were recovered from all 6 tags in the dataset. Nocturnal and diurnal depth distributions were nearly identical (Fig. 2A): about 60% of the time was spent in the top 10 m of the water column, > 80% was at depths of < 20 m, and only < 3% of the time was spent deeper than 50 m. Temperature data indicated that the sharks spent 72% of their time in water of 25–26 °C and encountered ambient temperatures of 20–32 °C (Fig. 2B).

The two individuals that moved west and northwest from the Bahamas behaved differently. Shark #40598 spent the first week in shallow waters (~ 10 m) and then moved to deeper waters in the second week (Fig. 3). Shark #40599 moved into deeper waters in the first week and then relatively shallow waters in the second week with its mean depth between 20–25 m. Both animals remained in shallow water for several days at a time, averaging about 10 m depth overall. Occasionally, both sharks engaged in periods of diving to depths of 50–90 m. Dives exceeding 30 m occurred equally often during day and night, and averaged just over 1.5 hrs in duration. These sharks spent 1.4–5% of their time below 30 m.

The depth trajectories of the two individuals that remained in the Bahamas were quite different from one another (Fig. 3). One shark, #40600, averaged 5.5 m depth and never exceeded 17 m. This individual remained in the immediate vicinity of Walker's Cay and was resighted 16 days after tagging. The other shark, #40597, showed a diving pattern more similar to the two animals that left the Bahamas (Fig. 3). Its average dive duration was somewhat shorter, at 1.1 hrs, and it spent 4% of its time below 30 m. This shark was recorded to dive to a maximum depth of 140 m on 11 April 2003 at 0200 h (Fig. 3) which is, to our knowledge, the greatest depth ever recorded for a bull shark.

DISCUSSION

All six tags popped up due to the optional constant pressure release mechanism. This resulted in a loss of valuable data but illustrates an important trade-off to consider when working with this relatively new technology. The automatic release mechanism could be switched off when working with marine animals that are known to stay at a constant depth for a longer time period. However, such behavioral traits are hard to confirm for many species, and even then switching off the automatic release mechanism can result in data loss because the tag will not detach from the animal when it dives to great depths or dies and sinks to the bottom. This can result in the complete loss of data stored in the expensive device.

Two sharks left the Bahamas and traveled toward Florida. Shark #40598 was observed at Walker's Cay on the day following tagging, and its tag popped up after 12 days on the Florida east coast (Fig. 1). The tag was found floating on the surface in the Stuart Inlet, about 210 km west of Walker's Cay. This area, at the entrance to the Indian and St. Lucie rivers, is a known nursery ground for bull sharks (Snelson and Williams, 1981; Snelson et al., 1984). Large females enter these shallow waters between late April and July to give birth (Snelson et al., 1984). This observation suggests that some female bull sharks from the Walker's Cay aggregation move to nursery grounds on the Florida coast.

The bull shark is considered a coastal species, but our data highlight a lack of good data on the ecological niche of this species. We found that bull sharks cross deeper waters, and that their behavior in open ocean may be similar to that of pelagic sharks. Depth and temperature data show that the sharks generally remained in shallow water (Fig. 2), consistent with earlier reports of bull sharks in shallow coastal waters (Compagno, 1984; Last and Stevens, 1994). However, the behavior of individuals that entered the open ocean was similar to that of other pelagic shark species. The three animals that left Walker's Cay, including two that moved westward and one that remained in the region, spent most time within 30 m of the surface, with occasional deep dives to 100 m or more. Similar diving patterns are known for pelagic species such as blue (Carey and Scharold, 1990) and mako sharks (Carey et al., 1981) and several explanations for oscillatory swimming are under discussion (Klimley et al., 2002).

This study was limited in the number of specimens tagged and duration of tracks. But our finding of movement of bull sharks between the Bahamas and Florida is important because it illustrates two key issues in marine conservation. First, spatially distinct habitats are often important at different times of year for large, mobile marine vertebrates. Scientists and government agencies must include these different habitats in their planning. Second, these animals can move considerable distances between habitats, and their migratory paths can

easily cross national borders. This underscores the need for international cooperation in devising conservation plans.

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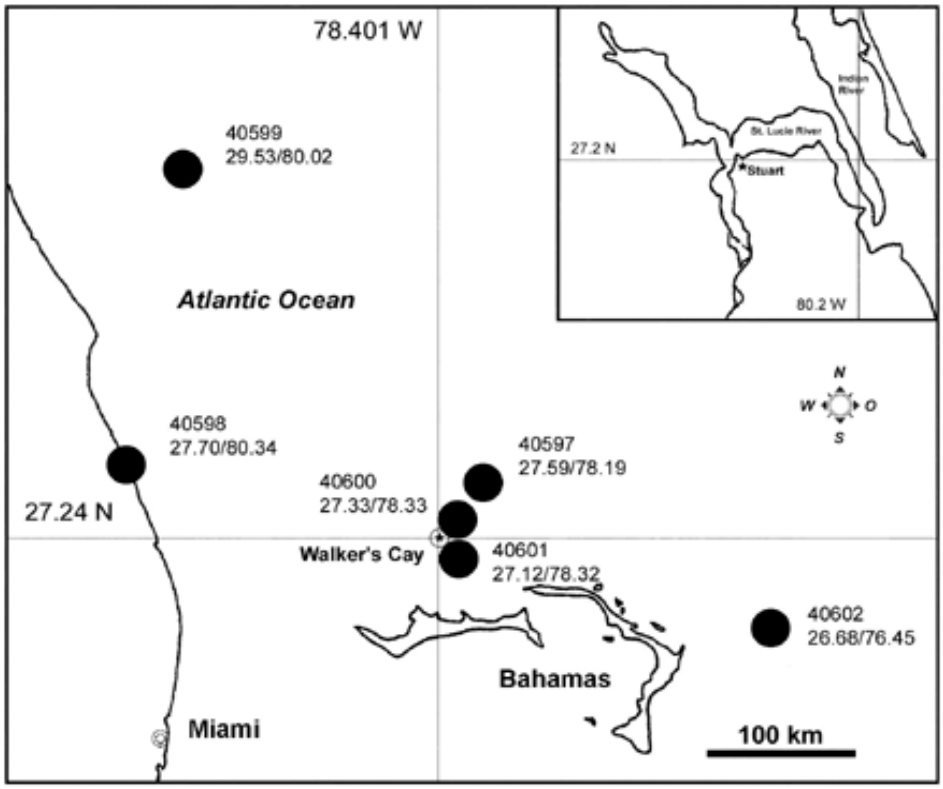

Figure 1. Pop-up locations of the six tags. The numbers next to each pop-up location signify the tag number (above) and the latitude and longitude at which pop-up occurred (below). Position of attachment (Walker's Cay) is marked with a circled star. The inset shows the Stuart inlet area where tag #40598 was found floating on the surface.

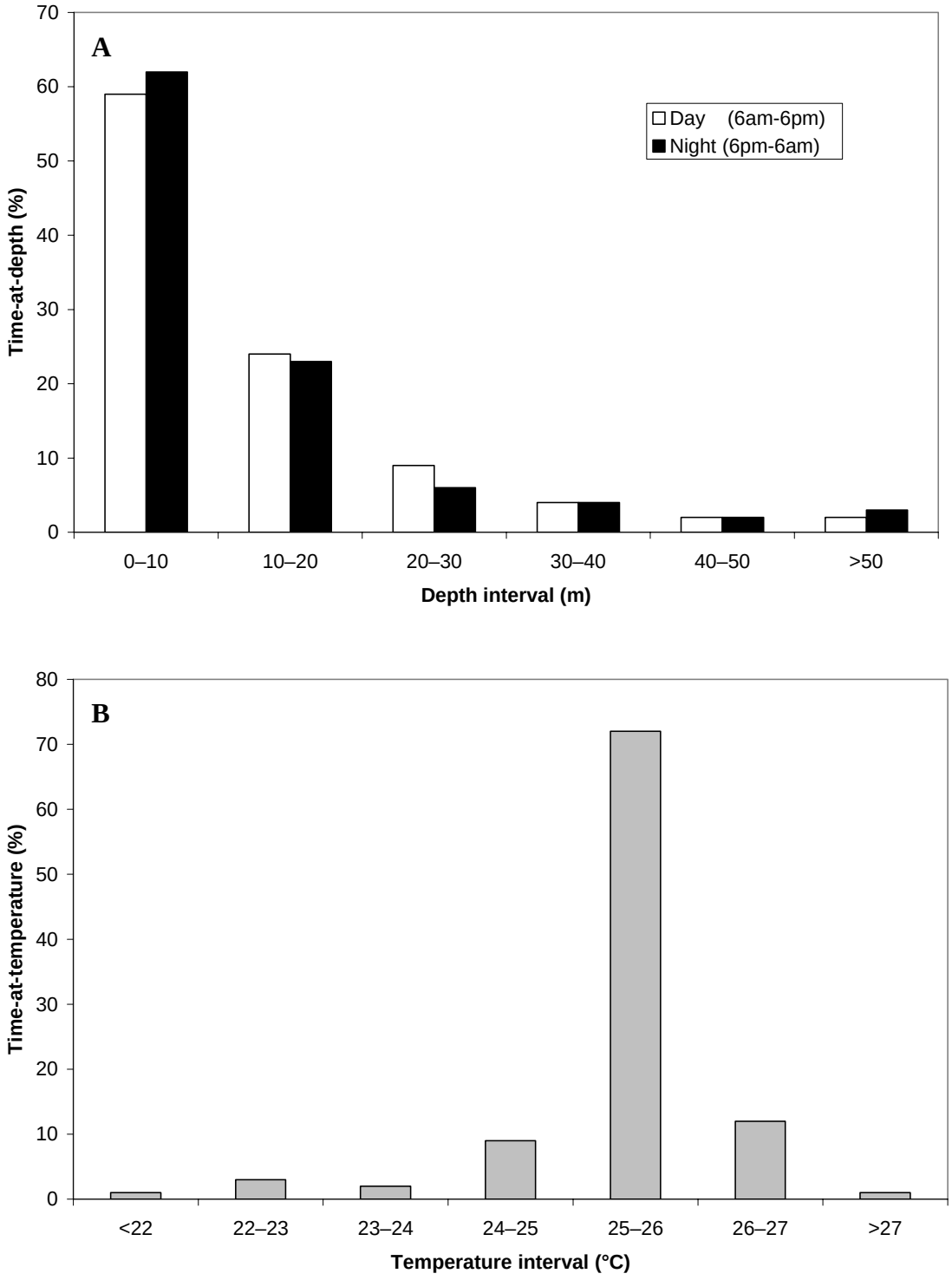

Figure 2. Frequency distributions of the time spent by all 6 bull sharks at different depths (A) and temperatures (B).

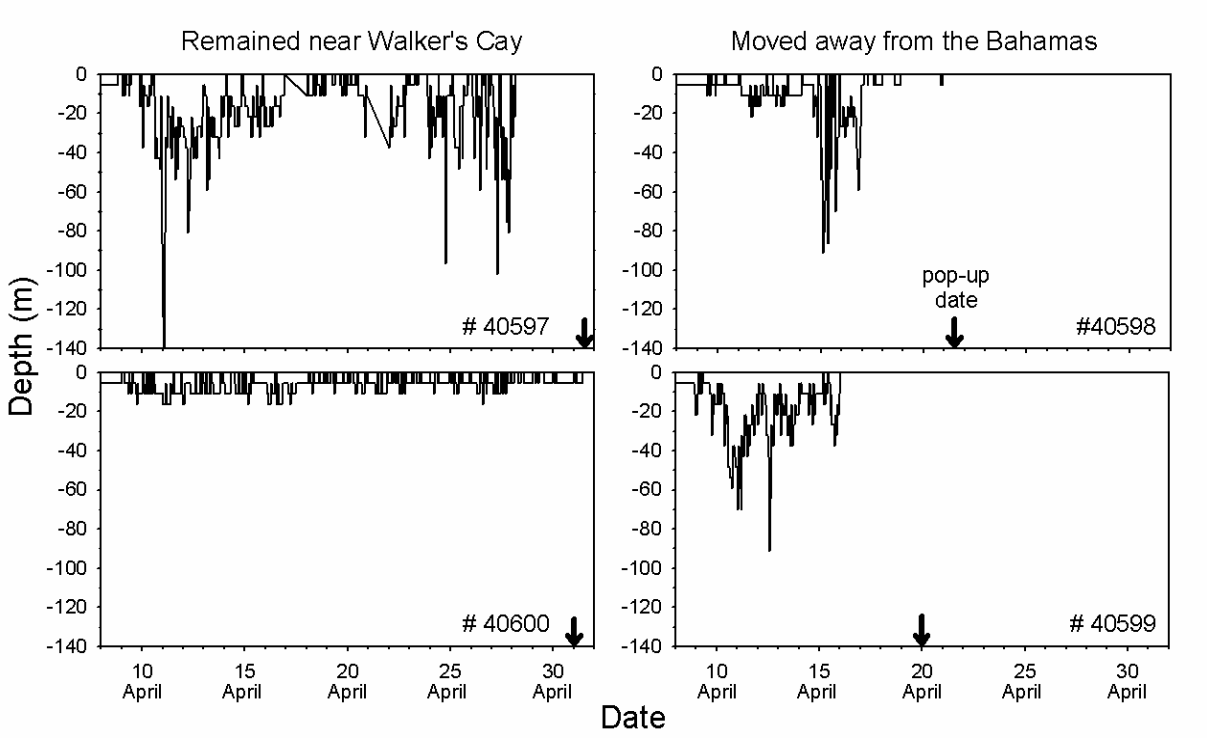

Figure 3. Depth records for four bull sharks tagged at Walker's Cay, Bahamas, on 8 April 2003. Sharks in the left-hand panels remained near the tagging site, whereas those in the right-hand panels moved west and northwest from the Bahamas. Pop-up dates are indicated by arrows.

Bull shark depth and temperature data from the South Pacific as determined by satellite telemetry

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A bull shark (*Carcharhinus leucas*) carrying a pop-up satellite archival tag. © Harald Baensch

ABSTRACT

Bull sharks, *Carcharhinus leucas*, were equipped with pop-up satellite archival tags (PSATs) at Shark Reef Marine Reserve, Fiji, to study their horizontal and vertical movements. All 11 PSATs (nine female sharks, two males) detached prematurely and no pop-up positions were available due to the disabled constant pressure release feature. Depth and temperature data while the tags were attached showed that most time was spent in water <50 m and 26-27 °C with only occasional deeper dives to a maximum depth of 204.4 m. Bull sharks remained deeper during the day than at night. These data help to better define the ecological niche of the bull shark and support conservation efforts for this species.

INTRODUCTION

Many recent studies document decreasing population trends and species loss of elasmobranch fishes (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005; Worm et al. 2005). Sharks and rays are vulnerable to anthropogenic threats such as commercial exploitation, physical habitat alteration, and pollution, because their life histories are characterized by slow growth, late maturity, long gestation, low fecundity, and high adult survival (Cailliet et al. 2005). Unfortunately, knowledge of elasmobranch ecology and behaviour lags behind that for most other large vertebrates, and this impedes efforts to counteract population declines. Newly-emerging technologies such as satellite technology can be powerful tools to collect much needed behavioural and ecological data from elasmobranchs.

Pop-up satellite archival tags (PSATs) have proven to be a valuable tool for marine biologists to understand habitat use and to better define the ecological niches of various marine predators (Block 2005). Problems that are thought to contribute to tag failure include anchor design or material, tissue rejection, electronic component failures, tag shedding by the animal, and attachment method (e.g. handling the animal in the water or on a boat). In the case of sharks, PSATs have mainly been attached to large pelagic species (Bonfil et al. 2005; Sims et al. 2005; Weng et al. 2005; Wilson et al. 2006). Coastal and reef species have rarely been outfitted with PSATs because the tag is large enough to cause a potentially important energy cost to the study animal (Grusha and Patterson 2005). It has also been thought that premature release is more likely in coastal and reef sharks, although this concern may be unfounded.

An alternative type of tag, archival tags, has been used to study habitat use in school sharks, *Galeorhinus galeus* (West and Stevens 2001). Traditional archival tags return data of high quality, but a large drawback is the need to recapture tagged animals to retrieve the data.

PSATs eliminate the need to recapture animals, but the data may be of poor quality for coastal and reef shark species because the animals do not move great distances. This paper reports data from PSAT tagged bull sharks, *Carcharhinus leucas*, at Shark Reef Marine Reserve (SRMR), Fiji. Virtually nothing is known about the distribution and ecology of this species in the Indo-West Pacific Ocean (Last and Stevens 1994) and Shark Reef (SR) is among the few places in the region where bull sharks can be encountered in reasonable numbers year-round (Brunnschweiler and Earle 2006). Bull sharks are unusual among elasmobranchs in that they frequently enter brackish or fresh water (Compagno 1990). This implies that they may require different conservation strategies than are employed for the majority of sharks and rays. This study will help identify the ecological niche of this species, and can support the development of plans for elasmobranch conservation in Fiji and other areas of the world (Bazilchuk 2006).

MATERIALS AND METHODS

Field work was conducted during 2004 at SRMR, S 18°18', E 178°01', Fiji (Brunnschweiler and Earle 2006). 11 bull sharks (nine females, two males) were equipped with individually colour-marked PTT-100 pop-up satellite archival tags manufactured by Microwave Telemetry, Columbia, MD (Table I). Three tags deployed in April 2004 archived hourly light, temperature (increments of 0.2 °C), and pressure readings (increments of 5.4 m), and recorded time of sunrise and sunset for subsequent calculation of latitude and longitude. Tags attached in October 2004 (n=8) made the same measurements every 15 min. Error ranges for the temperature and pressure sensors were +/- 0.08 °C and +/- 2.7 m, respectively. Tags can withstand pressure at 2000 m, and had preset attachment durations between two and eight months (Table I).

PTT-100 PSATs have an optional automatic release feature whereby a tag pops off and begins to transmit when it senses that it has been at a constant depth for four days. Depth variations less than 20 m are regarded by the tag as constant depth. The purpose of this feature is to indicate when a fish is dead or a tag is detached, but the automatic release feature may initiate pop off also from a live fish if the animal remains in shallow water or within a narrow depth range for four days (Brunnschweiler and Van Buskirk 2006). In this study, the automatic release feature was disabled in all tags.

After detaching from the animal, PSATs float to the surface and uplink to the Argos satellite system to provide a final position of the tag, estimated from the Doppler shift of the transmitted radio frequency in successive uplinks. The tag transmits a message consisting of 31 bytes at a time and the message contains sunrise and sunset times, checksums, and either

pressure or temperature data but not both in a single message. Although the data are stored chronologically in the tag, they are transmitted in a random order to ensure an even distribution of the data set. The tag continues transmitting for 10 to 30 days until all battery power is expended.

I deployed tags without catching the animals. Sharks were attracted with food to an area ~30 m deep at the edge of the reef, and a SCUBA diver drove the tag into the dorsal musculature below the first dorsal fin using a custom made tagging pole or a spear gun. The full setup consisted of the PSAT unit, a monofilament line marked with an individually coloured plastic tube, and a double barbed stainless steel anchor. Tagging was apparently not stressful, because all tagged sharks remained in the area and showed normal behaviour. On the days following attachment, the site was checked to see if tagged animals remained in the area. The size of each shark was estimated visually: medium (1.5–2.5 m), and large (2.5–3.5 m). Only animals >1.5 m were tagged.

RESULTS

All PSATs detached prematurely, having remained on the sharks for 1 to 53 days (mean = 18; Table I). Accurate pop-up position data are not available and no level of accuracy can be assigned because the tags floated for some time after detaching and before uplinking to the satellites. This is because the constant pressure release feature was switched off, and therefore the tag uplinked to the satellites only after the programmed pop-up date was reached (Microwave Telemetry, personal communication). The actual pop-up date and time was taken to be the point at which depth readings were constantly 0 m.

Tags differed in the extent to which they reported data. For example, although PSAT A2 remained attached to the shark for 17 days, only 1.5% of the pressure data are available for analysis. For PSAT O5, 89.7% of pressure data are available (Table I). PSAT A3 failed to report any data. Location estimates are available from only four tags and each of these only reported back a fraction of the archived geolocation data: PSAT O2 = five latitude/longitude estimates; PSAT O3 = one latitude and 13 longitude estimates; PSAT O5 = one latitude and five longitude estimates; PSAT O8 = 36 latitude/longitude estimates. The accuracy of light level geolocation estimates and especially latitude estimates is subject to considerable errors (Teo et al. 2004), which in the present study is confirmed by the following observation: the 36 latitude and longitude estimates of PSAT O8 indicated that the shark moved south reaching its southernmost point on 22 October 2004, 725 km south of the tagging site. However, this shark was positively identified based on the individually coloured plastic tube at the tagging

site the same day and occasionally for the following two weeks. Therefore, the few available position estimates are excluded from the analysis.

Nine tags reported depth data, recorded at one-hour intervals (PSAT A2) and 15 min intervals (PSAT O1–O8; Table II). Mean diving depth was 32.7 m (day = 34.4 m; night = 30.9 m). Depths were generally greater during the day than at night (Figure 1; $\chi^2 = 328.23$; df = 5; $p < 0.001$). Bull sharks spent about 63% of the time at >30 m depth during the day, but only 48% of the time below 30 m at night (e.g. PSAT O3 and O5; Figure 2a,b). About 10% of the time was spent deeper than 50 m and occasional deep dives were made to a maximum depth of 204.4 m (PSAT O8 on 27 November 2004 at 0330; Table I). This depth corresponded with the lowest measured ambient temperature of 21.37 °C. Individual depth data for the animal with the tag attached longest (PSAT O8; Table I) confirms this overall finding: the female bull shark was generally deeper during the day than at night ($\chi^2 = 133.96$; df = 5; $p < 0.001$), spending 80% of the time at greater than 30 m depth during the day versus 56% of the time below 30 m at night (Figure 2c).

Temperature data were recovered from nine tags (PSAT A2 and PSAT O1–O8). Ambient temperatures were 21.4–28.6 °C (mean = 26.04 °C; Table I), and the majority of the time (67%) was spent in water of 26–27 °C (Figure 3). Day and night temperatures were nearly identical.

DISCUSSION

The 154 days of bull shark depth and temperature data collected using PSATs help refine understanding of the ecological niche of the bull shark and contribute to local and international conservation efforts for this species. The bull shark is described as a coastal, estuarine, and riverine species usually found in water less than 30 m deep (Compagno 1984). The PSAT data show that bull sharks spend the majority of their time in water <50 m but make occasional dives to below 100 m. The maximum depth of 204 m (Table I) recorded in this study is the greatest depth ever directly measured for this species.

Bull sharks generally stayed in deeper water during the day than at night (Figure 1). Other elasmobranch species also exhibit changes in diurnal activity and show diel vertical movement patterns (Nelson et al. 1997; Loefer et al. 2005; Stokesbury et al. 2005; Sims et al. 2006; Wilson et al. 2006). Higher activity levels at night have been reported for many species (Nelson and Johnson 1970; Gruber et al. 1988; Parsons and Carlson 1998; Sims et al. 2006). Although foraging behaviour was not directly measured in this study, the depth data support the conclusion that bull sharks might use shallow habitats to forage at night. Bull sharks take

a very broad range of food, from bony fishes, invertebrates and elasmobranchs to sea turtles, birds and mammals (Snelson et al. 1984; Cortés 1999; Gannon et al. 2005). Many of these prey are most abundant in shallow nearshore environments (Heithaus et al. 2002).

Temperature data found in this study were in the same range as for bull sharks in the Bahamas (Brunnschweiler and Van Buskirk 2006). Sea surface temperature for Fiji is around 27 °C during October (http://www.ssec.wisc.edu/data/sst/archive/) and water temperatures between 40 m and the surface are between 25 and 28 °C (Brunnschweiler; unpublished data). Although ambient temperature is a key variable and plays a major role in controlling metabolic rates of ectothermic elasmobranchs (Carlson et al. 2004), I conclude that ambient temperature is not a key factor for different vertical depth distribution between day and night (Figure 1). However, the resolution of the temperature differences found in this study might not be sufficient to detect differences between day and night. Ectothermic sharks posses thermoreceptors capable of detecting temperature differences down to about 0.001°C (Brown 2003) and respond behaviourally to thermal gradients in the laboratory and field (Sims et al. 2006).

PSATs are best used with species that have broad spatial scales or in situations where location is of secondary importance because habitat use can be defined using depth and temperature data (Simpfendorfer and Heupel 2004). However, for poorly known shark species, information on long distance movements is unavailable prior to initial experience and studies. In this study, no data on the horizontal movement of bull sharks from SRMR are available because 1) no accurate pop-up positions are available due to premature detachment and disabling the constant pressure release feature and 2) only very few archived geolocation estimates were transmitted because battery life was too short to allow transmission of all archived data. Information on bull shark horizontal movement from Fiji would be valuable. At SRMR, the number of bull sharks decrease over the course of the year (Brunnschweiler and Earle 2006) and it remains a possibility that they show large-scale movements and use not only coastal habitat but also different marine habitats. It is well known that this species uses shallow mangrove areas as nursery grounds (Simpfendorfer et al. 2005) and can travel considerable distances to reach this habitat (Brunnschweiler and Van Buskirk 2006), but no nursery or mating grounds are yet confirmed for Fijian bull sharks.

The possibility of premature pop off due to the constant pressure release feature must be considered when working with poorly known marine vertebrates. Enabling the automatic release feature may result in premature pop offs and consequent loss of data (Brunnschweiler and Van Buskirk 2006), disabling the feature can also result in data loss. Premature release

due to, for example, tag shedding by the animal or inappropriate attachment results in the tag floating to the surface but not uplinking to the satellites until the programmed pop-up date has been reached. Opportunities accumulate for the tag to be eaten, covered in fouling organisms, washed up on a beach or otherwise damaged. Furthermore, no pop-up position is received and no "tag return" location is provided by the first accurately calculated position.

Are bull sharks suitable for pop-up satellite archival tagging? The vast majority of data published for PSAT tagged elasmobranchs are from large pelagic species. To date, a total of 17 bull sharks have been equipped with PSATs (Brunnschweiler and Van Buskirk 2006; this study). From these, only one tag (PSAT A3; Table I) failed to report any data. Most tags for which data are available remained on the shark for only a short time period and little position data are available (Table I; Brunnschweiler and Van Buskirk 2006). The available results show that premature releases are a serious issue to consider when working with this and probably other coastal species. Despite all the technical challenges, PSATs are a promising tool to study the behaviour of coastal shark species.

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Table I. Summary of 11 PSAT deployments and detachment for 11 bull sharks. All deployments took place at Shark Reef Marine Reserve, Fiji, at 18°18' S, 178°01' E. Size classes are based on visual size estimates: 2 = 1.5 – 2.5, 3 = 2.5 – 3.5 m. NA, data not available.

Tag no. Outcome	Size class	Sex	Deploy date (prg. pop-up date)	Pop-up date	Duration of deployment (d)	Pressure data		Temperature data	
						Max. depth (m)	Available (%)	Range (°C)	Data available (%)
PSAT A1[bd]	2	F	18 Apr (30 Nov) 2004	18 Apr 2004	1	64.6	100	NA	NA
PSAT A2[b]	2	F	18 Apr (05 Dec) 2004	05 May 2004	17	53.8	1.5	26.92 – 28.57	4.4
PSAT A3[ad]	3	M	23 Apr (20 Dec) 2004	NA	NA	NA	NA	NA	NA
PSAT O1[b]	3	F	01 Oct (30 Nov) 2004	09 Oct 2004	8	107.6	55.2	24.78 – 26.37	71
PSAT O2[c]	3	F	30 Sep (05 Dec) 2004	22 Oct 2004	22	96.8	28.5	24.25 – 26.01	25
PSAT O3[c]	2	F	04 Oct (20 Dec) 2004	28 Oct 2004	24	161.4	79.5	21.70 – 27.46	76.4
PSAT O4[b]	2	F	03 Oct (01 Dec) 2004	14 Oct 2004	11	96.8	55	24.60 – 27.28	66.1
PSAT O5[c]	2	M	01 Oct (10 Dec) 2004	20 Oct 2004	19	102.2	89.7	24.60 – 26.37	84.9
PSAT O6[b]	3	F	04 Oct (15 Dec) 2004	10 Oct 2004	6	102.2	79.8	25.48 – 26.37	79.3
PSAT O7[b]	2	F	06 Oct (25 Dec) 2004	11 Oct 2004	5	48.4	25.4	25.84 – 26.37	20.3
PSAT O8[c]	2	F	06 Oct (30 Dec) 2004	28 Nov 2004	53	204.4	28.5	21.37 – 28.39	33.2

[a] Tag failed to report position estimates and data
[b] Tag reported data but failed to report position estimates
[c] Tag reported data and position estimates
[d] Excluded from analysis

Table II. Summary of depth (m) data for nine sharks. Mean diving depth (±SD) was 34.4 m (14.8) during the day (6 am – 6 pm) and 30.9 m (18.5) during the night (6 pm – 6 am).

	# Readings			Mean depth (SD)		% time-at-depth day / night					
Tag no.	Day	Night	Mean depth (SD)	Day	Night	0-10	10-20	20-30	30-40	40-50	>50
PSAT A2	12	12	33.4 (9.2)	32.7 (7.1)	34.1 (11.3)	0 / 0	8.3 / 8.3	16.7 / 33.4	66.7 / 25	8.3 / 25	0 / 8.3
PSAT O1	220	218	29.5 (9.6)	29.5 (6.8)	29.4 (11.8)	0 / 0.9	1.4 / 11.5	60 / 43.6	36.4 / 35.3	1.7 / 5.5	0.5 / 3.2
PSAT O2	300	300	30.7 (13.7)	35.6 (12.5)	25.8 (13.1)	0 / 6.7	5.7 / 22.3	23.6 / 35.3	43.7 / 26	20 / 6	7 / 3.7
PSAT O3	934	917	35 (22.2)	34 (20.7)	36 (23.6)	3.9 / 8.8	19.1 / 14.3	26.2 / 22.8	21.1 / 18.3	14 / 14	15.7 / 21.8
PSAT O4	302	291	33.1 (16.5)	38.8 (16.5)	27.1 (14.2)	0 / 5.8	2.3 / 22.3	31.8 / 33	28.5 / 24.1	18.2 / 8.9	19.2 / 5.9
PSAT O5	837	823	28.4 (11.4)	31.1 (9.2)	25.7 (12.7)	0.4 / 6.4	5.6 / 23.2	36.9 / 35.5	47.4 / 24.9	6.8 / 6.6	2.6 / 3.4
PSAT O6	219	228	36.1 (11.1)	37.2 (9.5)	34.9 (12.3)	0.9 / 0.9	3.2 / 5.3	12.8 / 20.2	46.1 / 54.8	32 / 14.9	5 / 3.9
PSAT O7	60	60	34.3 (6.4)	35.4 (6.6)	33.2 (6.1)	0 / 0	1.6 / 0	15 / 26.7	66.7 / 60	16.7 / 13.3	0 / 0
PSAT O8	731	727	34.9 (18.1)	37 (13.4)	32.8 (21.7)	2.6 / 11.6	2.9 / 12	15.5 / 20.4	51.3 / 30	16.8 / 12.7	10.9 / 13.3

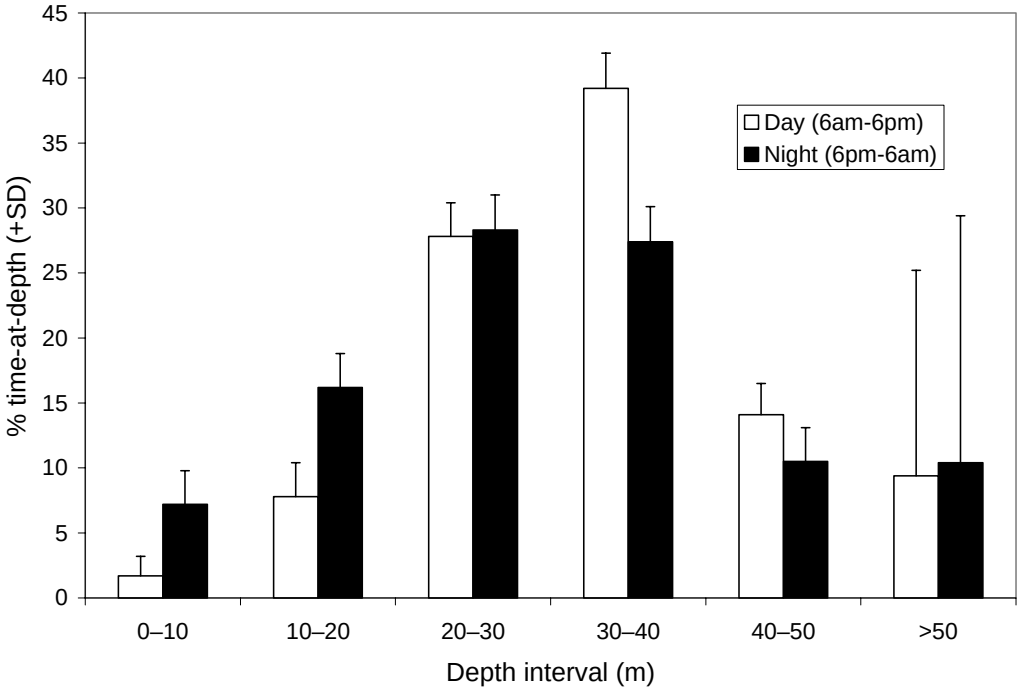

Figure 1. Histogram showing percentage time-at-depth, pooled across the nine sharks. Sharks generally stayed deeper during the day than at night.

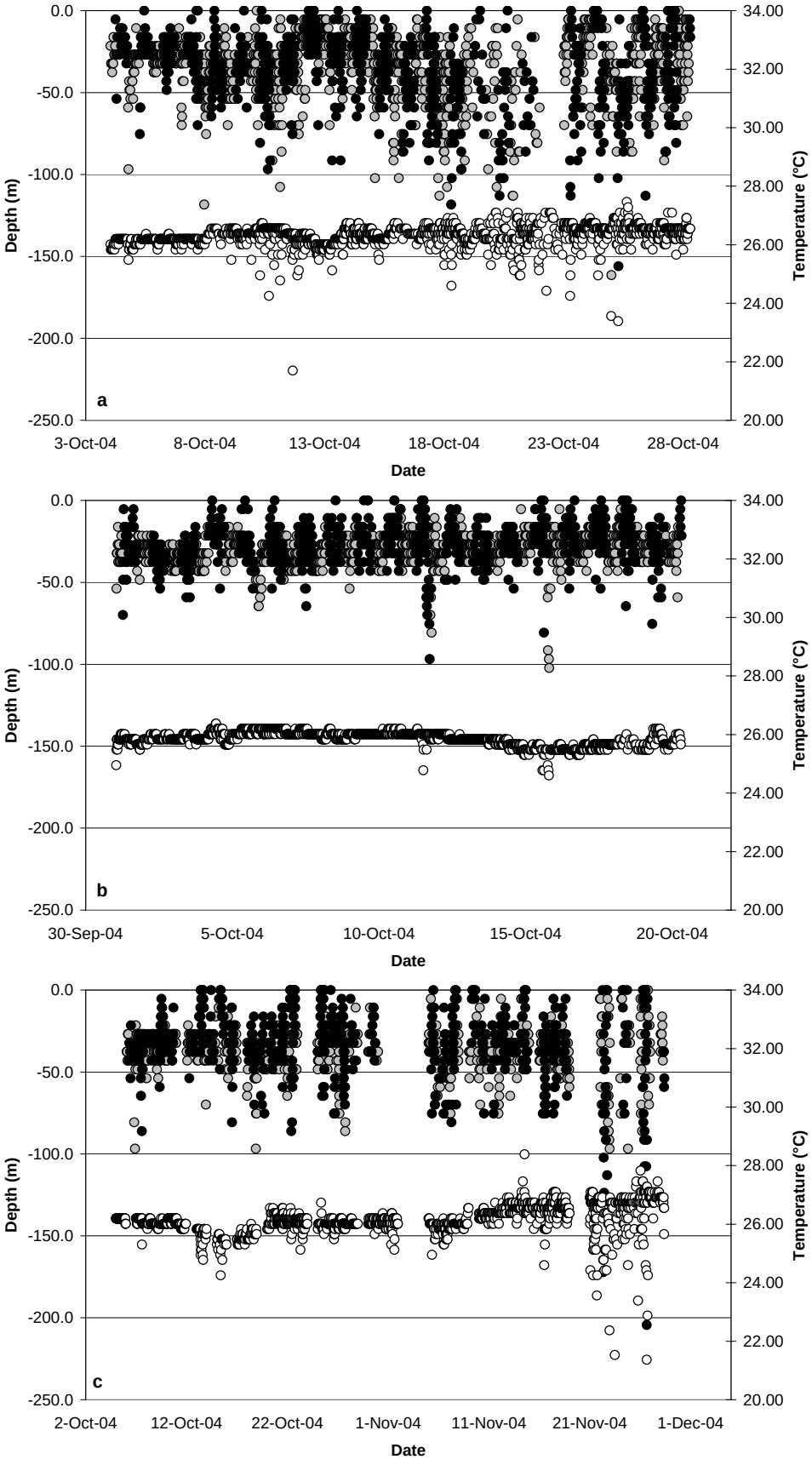

Figure 2. Depth and ambient temperature profile for a) PSAT O3, b) PSAT O5, and c) PSAT O8. Grey dots = day depth; black dots = night depth; white dots = temperature. The majority of the time was spent in water <50 m with occasional deeper dives.

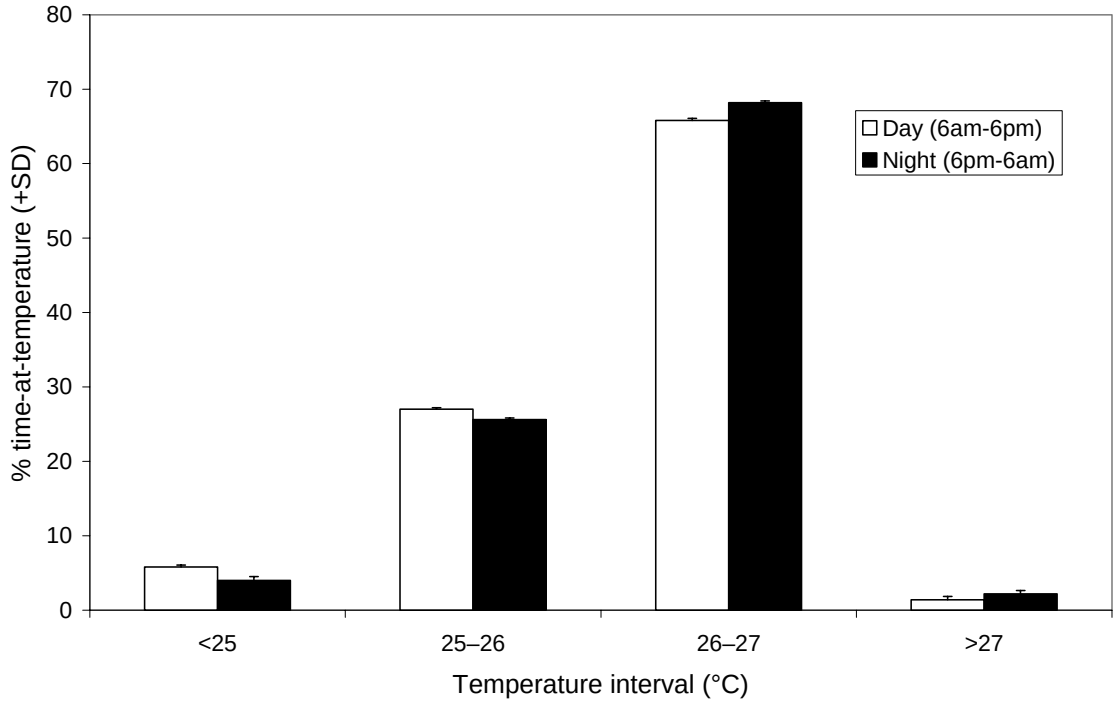

Figure 3. Histogram showing percentage time-at-temperature, pooled across the nine sharks. The majority of time was spent in water of 26–27 °C. Bull sharks experienced the same water temperatures during night and day.

Depth and temperature data from a whale shark crossing the Mozambique Channel

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A whale shark (*Rhincodon typus*) off the coast of Mozambique carrying a pop-up satellite archival tag and a conventional visual tag. © Harald Baensch

ABSTRACT

A whale shark *Rhincodon typus* crossing the Mozambique Channel from Mozambique to Madagascar spent most of the time near the water surface but showed occasional deep dives to a maximum depth of 1286 m. Ambient temperature range was 26.52 °C.

Whale sharks *Rhincondon typus* (Smith) play an important role in socio-economic activities in many parts of the world because they are harvested by fisheries and targeted heavily for ecotourism (Davis *et al*., 1997; Clarke *et al*., 2005; Stewart & Wilson, 2005). Detailed knowledge of the biology and ecology of the whale shark is limited, although much has been learnt since Colman's review in 1997. The long-term movements of the whale shark are among the best studied of any elasmobranch. Whale sharks satellite-tagged in the Sea of Cortez, in South-east Asia, and off Western Australia, travelled distances of thousands of kilometres, moving through multiple political jurisdictions (Eckert & Stewart, 2001; Eckert *et al*., 2002; Wilson *et al*. 2006). A key factor in sustainable management of socio-economic activities is a detailed understanding of vertical and horizontal movement patterns which contribute to a better understanding of the still little known habitat of this planktivorous species. Despite an increasing amount of data on large-scale movement patterns in whale sharks, information on habitat use away from shallow-water feeding grounds is lacking, especially in poorly-studied geographic regions. Here, data on horizontal and vertical movement of a whale shark crossing the Mozambique Channel are presented.

On 18 February 2006 a female whale shark was equipped with a pop-up satellite archival tag (PTT-100, Microwave Telemetry, Columbia MD) at S 24.106°, E 35.504°, south-east of Tofo, Mozambique. The size of the shark was visually estimated to be 6 to 7 m using the length of the research vessel as reference. The shark was approached by a snorkler and the tag was driven into the dorsal musculature between the first and the second dorsal fins using a spear gun. The tag archived light, temperature and pressure readings every 15 min and recorded time of sunrise and sunset for subsequent calculation of latitude and longitude. Error ranges for the temperature and pressure sensors were +/- 0.08 °C and +/- 2.7 m, respectively. The tag was programmed to pop-up on 30 November 2006.

The tag popped up prematurely 91 days after attachment on 20 May 2006 at S 24.224°, E 47.639° (location class 2; Hays *et al*., 2001), on the south-east coast of Madagascar. The archived data were transmitted via the Argos satellite system (Block, 2005) and a total of 52% of the collected data were retrieved. Available temperature and pressure readings were used to analyse the vertical movement of the shark. Unfortunately, only a few

light level latitude estimates were successfully downloaded. However, light level longitude estimates are available, and these are typically accurate and robust (Teo *et al*., 2004). Therefore, the horizontal eastward movement of the shark crossing the Mozambique Channel are described using only longitude values averaged over 5-day periods. All times reported here (unless noted) are GMT.

The movement of the whale shark from Mozambique to the east coast of Madagascar can be divided into 5 phases (Fig. 1). For the first 22 days after tagging (18 February to 11 March, phase I), the shark stayed close to the coast at the surface, with only occasional deeper dives to a maximum depth of 69.9 m (Fig. 2A). The mean diving depth during this time period was 11.4 m (SD = 17.3 m) and mean water temperature 27.4 °C. A first dive below 100 m was recorded on 6 March and regular deep diving was observed from 12 March onwards (Fig. 2A).

The shark moved away from the coast in mid March (Fig. 1), entering the deep (>2000 m) waters of the Mozambique Channel (Smith & Sandwell, 1997). During this second phase (12 March to 7 April), the mean diving depth was 104.5 m (SD = 145 m) and mean temperature 21.8 °C. The shark reached the longitude E 43° at the beginning of April (Fig. 1) and then swam against the East Madagascar Current crossing the shallower (<2000 m) plateau south of Madagascar (Quartly & Srokosz, 2004). This third phase (08 April to 15 April) was characterized by a mean diving depth of 27 m (SD = 50.6 m) and a mean temperature of 24.6 °C. The whale shark moved further east into deep water after passing southern Madagascar in mid-April, reaching a maximum longitude of E 50.5° on 4 and 5 May. It then returned towards the east coast of Madagascar, where pop-up occurred on 20 May (Fig. 1). Phase IV (16 April to 16 May) was characterized by a mean diving depht of 78.4 m (SD = 126.8 m) and a mean temperature of 23.2 °C. Four days before pop-up, the shark stopped diving and stayed close to the surface (Fig. 2A) which activated a constant pressure release mechanism (Brunnschweiler & Van Buskirk, 2006).

Point to point distance travelled by the whale shark within 91 days between Mozambique and the east coast of Madagascar was 1232 km. Mean movement rate was therefore at least 13.5 km/day. However, the shark spent some time close to the coast before moving eastwards, so the deepest portion of the Mozambique Channel (Quartly & Srokosz, 2004) was crossed with a minimum speed of 24.4 km/day. Similar minimum speeds have been found in other studies of whale shark movements (Eckert & Stewart, 2001; Eckert *et al*., 2002; Wilson *et al*., 2006).

87% of the archived pressure (= 7607 data points; Fig. 2A) and temperature readings (= 7657 points; Fig. 2B) are available and summarised in Figs 3 and 4. The shark spent the majority of its time in water 0 to 100 m deep (mean depth = 61.3 m). Comparing the 100 m intervals, depths were generally greater during the day than at night (Chi-Square test, d.f. = 5, $p < 0.001$). The shark spent 91.4% of the time in water <100 m during the night, but only 69.7% during the day (Fig. 3). Within the first 100 m of the water column, the whale shark spent the majority of the time in water 0 to 10 m deep (Fig. 3; 73.1% during the day *versus* 53.9% at night) and most of the daytime was spent in the upper water column when comparing the 10 m intervals (Chi-Square test, d.f. 9, $p < 0.001$). Diving behaviour for *R. typus* has been found to be similar in other studies (Gunn *et al*., 1999; Graham *et al*., 2005). This diel change in preferred depth is consistent with a response to food patches that occupy deeper depth strata during the day (Sims *et al*., 2003).

Ambient temperatures were 3.38 to 29.9 °C (mean = 23.98 °C), and 53.1% of the time was spent in water of 24 to 28 °C (Fig. 4). The temperature range of 26.5 °C is only slightly larger than previously reported for this species (Graham *et al*., 2005) and whale sharks are known to tolerate cold temperatures (Turnbull & Randell, 2006).

A total of 5 dives below 1000 m were recorded (20 and 23 March and 18 April). The two deepest dives were observed on 20 March and 18 April with 1264.2 and 1285.7 m at 1815 and 0015, respectively (Fig. 2; Fig. 2A). These two depths corresponded with the lowest measured ambient temperatures of 4.2 and 3.38 °C (Fig. 2B). At 1730 on 20 March the shark was at the surface and then dove down to 166.8 and 914.5 reaching 1264.2 m at 1815 (15 min intervals) with a minimum diving speed of 28.1 m/min. At 1830 the shark was at a depth of 699.3 m and stayed between 430.4 and 742.4 m for the next 30 min before it was recorded for a second time that day below 1000 m at 1915 (Fig. 2A). Similarly, one hour before the deepest dive reported here on 18 April, the whale shark was at the surface and then dove down to 145.2, 182.9 and 973.7 reaching a record depth of 1285.7 m at 0015 (15 min intervals) with a minimum diving speed of 21.4 m/min. For the next 45 min the shark stayed between 586.4 and 919.9 m before it made another dive to 1113.6 m at 0115 (Fig. 2A).

Previous studies have found that whale sharks dive to at least 980 m (Graham *et al*., 2005; Wilson *et al*., 2006). The maximum depth of 1285.7 m observed in this study is therefore the deepest diving depth ever directly recorded for this species. It remains unknown what exactly triggers such fast and short deep dives in this plankton-feeding elasmobranch. Whale sharks are often observed feeding close to the water surface (Clark & Nelson, 1997; Heyman *et al*., 2001), but the use of a broad vertical habitat, extending from the surface

across both epipelagic and mesopelagic zones over a time scale of hours, has also been found in basking sharks *Cetorhinus maxiums* (Gunnerus), another planktivorous shark that may be prospecting for zooplankton on irregular deep dives (Sims et al., 2003). Another plausible explanation for dives across different vertical depth strata is that they help the animal acquire navigational cues. Although little is known about how animals navigate over long distances (Alerstam, 2006), it has been suggested that sharks might explore the water column to gain directional information (Klimley et al., 2002). An even more speculative explanation for the deep dives is that the whale shark made use of favourable currents or avoided strong counter currents. Little data are available on the depth penetration of currents in the Mozambique Channel (Quartly & Srokosz, 2004), but this area is dominated by large eddies (~200 km diameter) and undercurrent flows equatorward.

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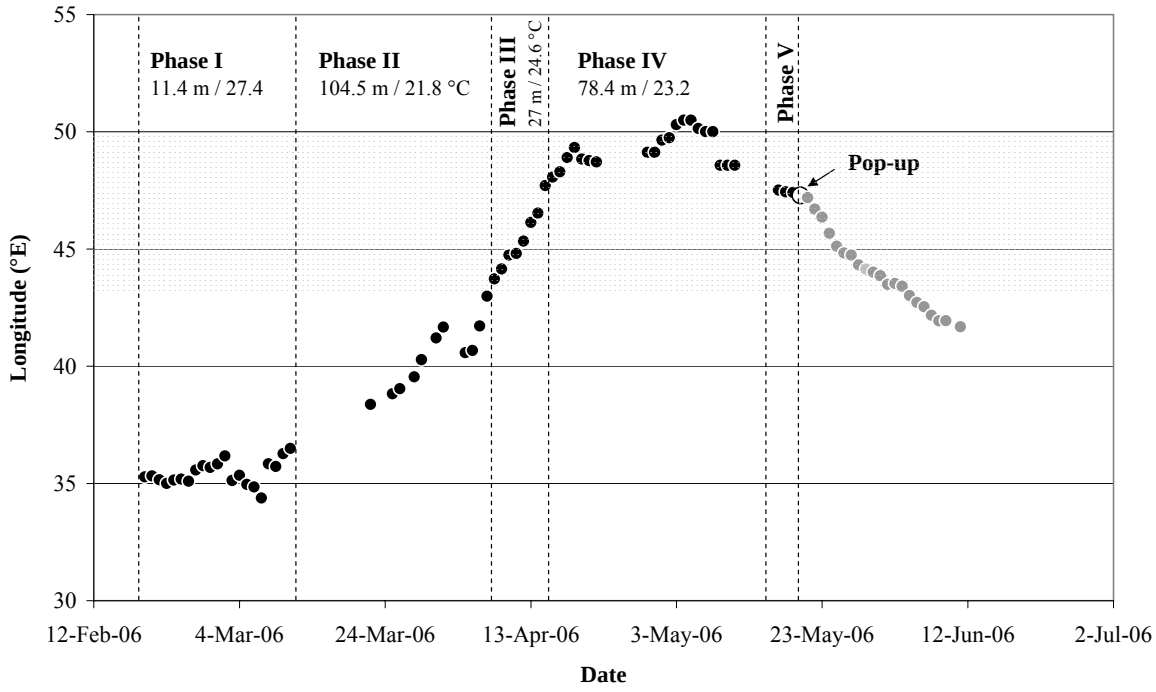

Figure 1. Longitudinal coordinates for a female whale shark satellite tagged off Mozambique. Black dots represent light-based longitude estimates averaged over a 5 day period; grey dots are Argos' longitude indicating the tag floating on the surface with the East Madagascar Current (Quartly & Srokosz, 2004). Pop-up location on 20 May is marked with a white dot. The grey shaded area represents Madagascar E 43° to 50°. The attachment period is divided into 5 phases with the first two representing the initial coastal phase and the crossing of the deep waters of the Mozambique Channel.

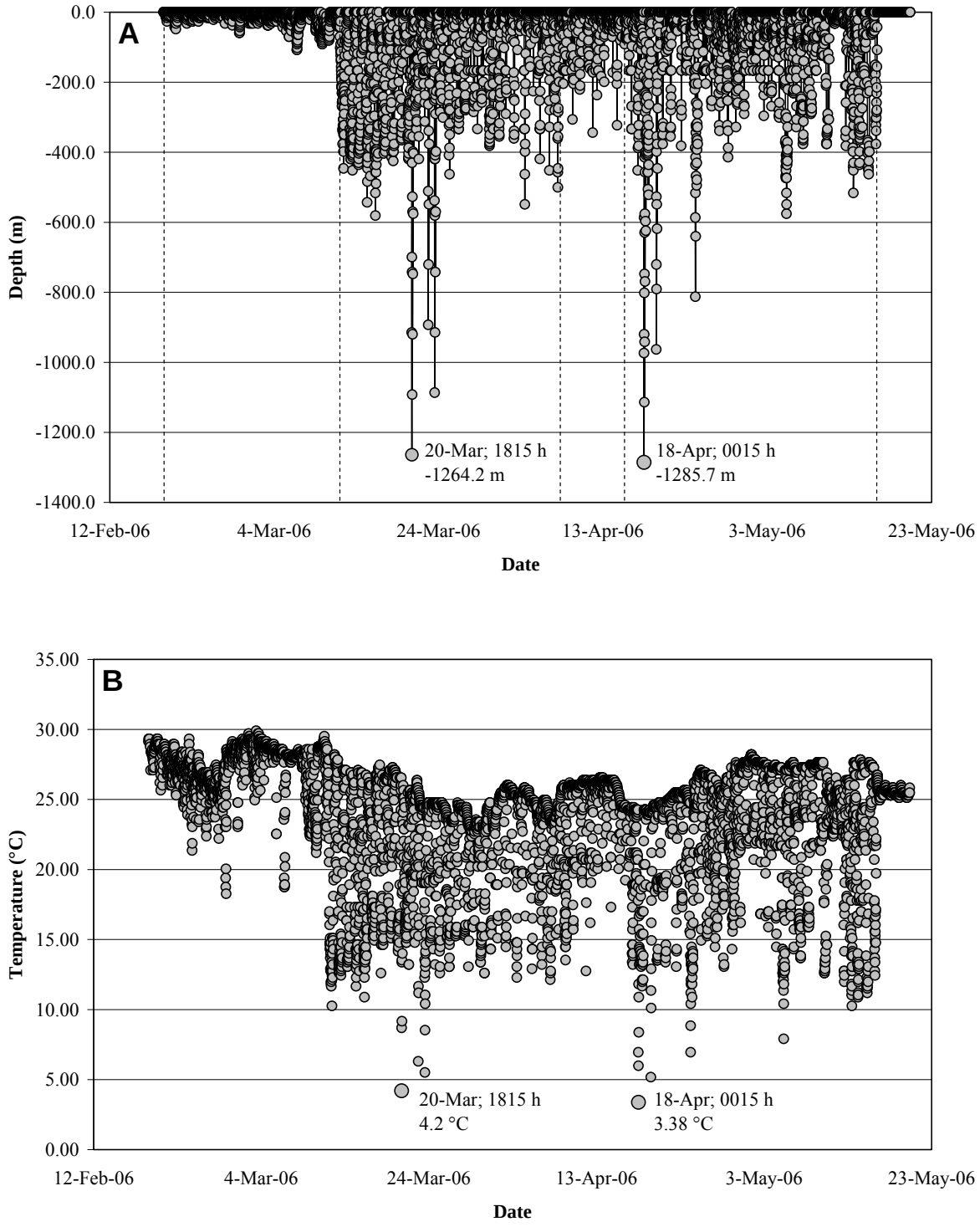

Figure 2. Depth (A) and temperature (B) profile of the female whale shark crossing the Mozambique Channel. The two deepest dives and their corresponding temperatures on 20 March and 18 April are labelled. Vertical dashed lines (A) correspond to the 5 movement phases (see text for details). Dives below 1000 m were only recorded in phases II and IV.

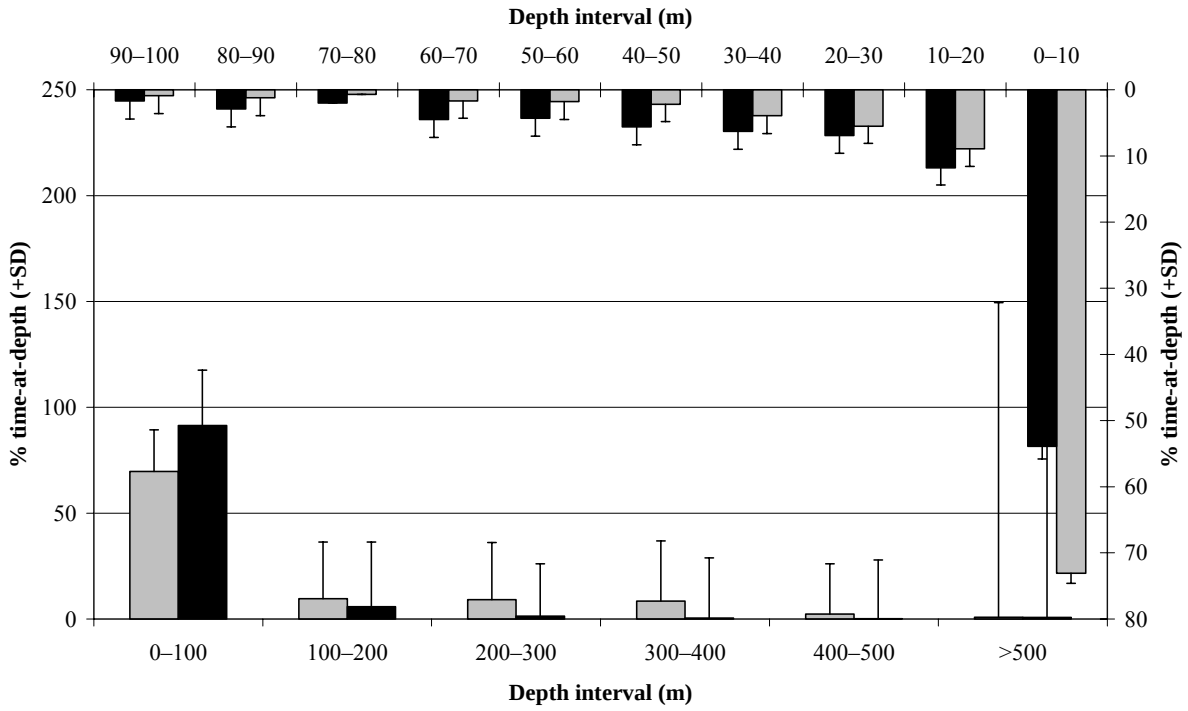

Figure 3. Histogram of percentage time-at-depth for 100 m intervals (n = 7607 data points; below) and 0 to 100 m (n = 6128 data points; above). Day (0600 to 1800; grey) and night (1800 to 0600; black) times are GMT + 2 hours. Overall, the shark stayed in deeper water during the day than at night and spent most of its time in the upper 100 m of the water column. When in the upper 100 m, the shark stayed deeper during the night.

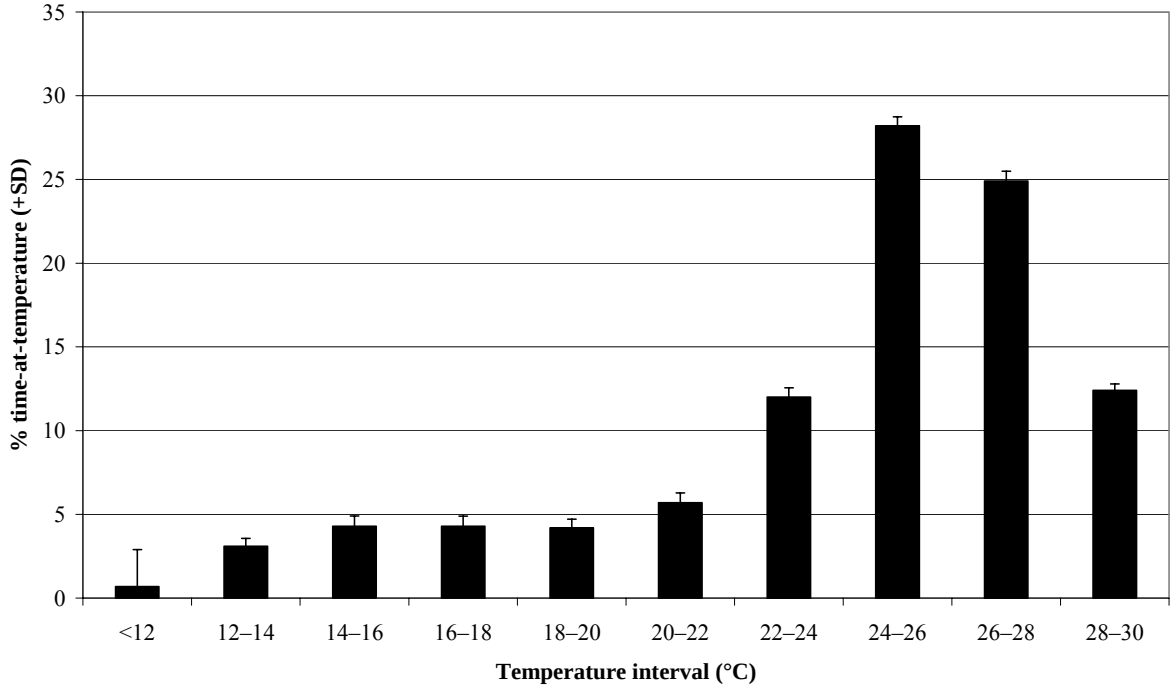

Figure 4. Histogram of percentage time-at-temperature of the whale shark moving from Mozambique to Madagascar. Most time was spent between 24 and 28 °C. Mean temperature 23.98 °C.

Appendix I – PTT 100 pop-up satellite archival tag

Archival satellite tags are increasingly used by researchers to study wide-ranging pelagic vertebrates. Because the ARGOS system uses polar-orbiting satellites, the position of the animal can be determined whenever it is at the surface when a satellite is overhead, no matter where in the world's oceans the animal is. The accuracy of position estimates is, at best, to within approximately 250 m of the true position, and in most marine animal studies many position estimates will be only within 10 km (Hays *et al*. 2001).

Archival tags store data on light level (for estimating the geographic position), depth, and temperature, and were developed to overcome the problems of collecting long-term data on animals that rarely, if ever, come to the surface. Because light levels are used to calculate positions (light-based geolocation), sunrise and sunset times, relative to Greenwich Mean Time (longitude), and day length (latitude) must be accurately estimated. Light-based geolocation gives inaccurate estimates of location (Welch & Eveson 1999). Therefore, archival tags are most useful when studying species that migrate long distances or in situations where location is of secondary importance. A major drawback of traditional archival tags is the need to recapture tagged animals to retrieve the stored data. In most cases, this is only possible when working with heavily exploited species that have high rates of recapture (Holland *et al*. 2001).

Pop-up satellite archival tags (PSATs) do not require recapture of the tagged animal, and there is no need to return the tag to a tagging agency. Therefore, far more information on movements can be obtained from fewer tagged animals (Sedberry & Loefer 2001). PSATs are particularly good at revealing large scale movements, water temperature ranges to which the animals are exposed, and the general swimming/depth pattern (e.g. Bonfil *et al*. 2005; Hulbert *et al*. 2006; Wilson *et al*. 2006). The results can provide excellent preliminary data that benefit from follow-up studies using other methods (Le Boeuf 2004).

Pop-up satellite archival tags used in the papers presented in this section all were PTT-100 manufactured by Microwave Telemetry, Inc., Columbia, MD. The unit is approximately 33 cm in length (including the 21 cm antenna), 4 cm in diameter at its widest point, and weights 68 g in air. It archives temperature, depth, and sunrise and sunset times for subsequent geolocation calculation. Tags are rated to withstand 3000psi (2000 m) and have an optional pressure initiated pop-off feature to allow the tag to pop off and start transmitting if it descends below a predetermined depth or remains at a constant depth over a predetermined length of time. Tags can be programmed to release either on a specific date or after a preset time on the shark. After pop-up, data are transmitted through the ARGOS satellite system.

Once on the surface, the tag uses a built-in radio transmitter to upload its archived data to satellites in the ARGOS system. The tag continues transmitting until all battery power is expended (10-30 days). The location of the transmitter is calculated from the Doppler shift in the frequency of transmissions received by a satellite as it approaches and then moves away from the transmitter on a single overpass, with each location being assigned a level of accuracy (<150 m to >1000 m; Hays *et al*. 2001). The integrating inclinometer readings recorded before and after pop-up together with data from the pressure sensor can be used to confirm that the tag was not free floating before pop-up.

A wide range of marine animals from different taxa have been studied using satellite technology, including bony (e.g. Wilson *et al*. 2005) and cartilaginous fishes (e.g. Bonfil *et al*. 2005), birds (e.g. Nicholls *et al*. 2002), reptiles (Hays *et al*. 2004) and marine mammals (Le Boeuf *et al*. 2000). However, the choice can be limited by the size of the device relative to the size of the animal. While satellite and archival tags are often small enough to use with smaller species (e.g. West & Stevens 2001), PSATs are large enough that they can be used only with relatively large marine animals. The major point of concern here is that some species or age groups may not be suitable candidates for carrying PSATs because of the potential energy cost to the study animal (Grusha & Patterson 2005).

Because satellite tags only uplink to the polar orbiting satellites when the antenna is on the water surface (the animal either swims at the water surface or the tag detaches from the animal and floats to the surface), tags have to be attached externally onto the animals. This leads to a range of problems that can contribute to tag failure, such as attachment technique, anchor design, and material and hydrodynamic properties of the device. In sharks, empirical data on attachment failure is still mostly lacking. In addition to attachment problems, there are many other possibilities for tag failure, such as physical damage, battery failure, electronic failure (failure to release), and biological issues such as predation by other fish or removal of the tag by the tagged animal itself. Longer tag deployment times typically reduce tag reporting success rates.

Premature pop off is a major drawback in many studies using PSATs on sharks. In many available studies, a few PSATs reported back data while many tags popped off prematurely, which resulted in less information (e.g. Bonfil *et al*. 2005; Wilson *et al*. 2006). Reasons for premature pop off are in most cases unclear but likely because of one of the above mentioned points. A technical aspect of the PTT-100 PSAT that has not yet been covered in the published literature is the optional constant pressure release mechanism.

PTT-100 archival pop-up tags are equipped with an optional automatic release feature, whereby a tag pops off and begins to transmit when it senses that it has been at a constant depth for four days. Depth variation <20 m is regarded by the tag as constant depth. The purpose of this feature is to indicate when a fish is dead or a tag is detached, but the automatic release feature may initiate pop off also from a live fish if the animal being tracked remains in shallow water or within a narrow depth range for four days (Brunnschweiler & Van Buskirk 2006).

The possibility of premature pop off due to the constant pressure release mechanism is a trade-off to consider when working with poorly known animals such as sharks. The automatic release feature can be disabled, but the manufacturer strongly suggests not doing this. However, when working with a coastal shark species it is very likely that the animals will stay at a constant depth for more than four days. In this case, enabling the automatic release feature may result in premature pop offs and consequent loss of data. Unfortunately, disabling the feature can also result in data loss. For example, a tag that is improperly anchored can detach from the fish and float to the surface, but not start uplinking to the satellites until the programmed pop-up date has been reached. Tags have a poorer reporting rate if they detach prematurely and float around for weeks or months before the programmed data transmission date. The opportunities for the tag to be eaten, covered in growth, washed up on a beach, or otherwise damaged reduce the chances of getting the archived data. More importantly, no pop-up position is received and no "tag return" location is provided by the first accurately calculated position. The first estimated position will only be available when the programmed pop-up date has been reached and until then, the tag can float on the surface considerable distances depending on the time lag between true pop off and programmed pop-up date. It is evident that this information has no biological meaning.

As previously noted, PSATs are a relatively new tool for marine biologists and only few studies using few different shark species are currently available. It is therefore difficult to make the right decision about enabling or disabling the automatic release feature. Given the high costs of PSATs, it is in most cases also not possible to use a large number of tags and enable/disable the feature in a certain proportion. While a certain risk remains with the researcher in all cases, pilot studies – especially when working with species not previously tagged with PSATs – might be a solution to at least reduce the risk of data loss. Furthermore, as more studies using PSATs become available, more information for different species will be available.

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Appendix II – Shark Reef Marine Reserve, Fiji

The first steps toward the establishment of what is known today as Shark Reef Marine Reserve (SRMR) were undertaken by a local dive operator in Pacific Harbour, Fiji, in 2003 (for map see Figure 1 on page 97). The initial goal was to reach an agreement with the traditional owners of the reef, residing in Wainiyabia Village, so that in exchange for the village not to fish on the reef, a local dive operator would collect a so-called "shark levy" of F$ 5 per diver per day to be transferred directly to the village. In April 2003 the project was endorsed by the Honorable Konisi Yabaki, Fijian Minister of Fisheries and Forestry. Subsequently, numerous meetings with the representatives of Wainiyabia Village have been held until a village committee was established and a joint bank account was established into which the "shark levy" is deposited. Simultaneously, a dive site was developed and maintained on Shark Reef and safety and other procedures for shark diving were developed.

In the fall of 2003, a different village (Galoa Village) raised claim that the traditional fishing rights to Shark Reef belong to them. All proceedings towards the establishment of Shark Reef Marine Reserve were halted pending the resolution of that issue. Numerous meetings were held with representatives of both villages under the guidance of the Principal Research Officer within the Fijian Department of Fisheries in order to mediate and resolve the contentious issue. In February 2004, a final agreement was reached whereby both villages jointly asked for the establishment of Shark Reef Marine Reserve. It was agreed that the "shark levy" would be equally split between the two villages.

On 8 April 2004, a formal meeting between the joint representatives of the two villages with representatives of the Ministry of Fisheries was held and it was formally decided to establish a marine reserve at Shark Reef. A single dive operator was assigned the exclusive rights to operate the shark dive and collect the "shark levy" in Pacific Harbour. It was agreed that all other dive operators would be welcome to join in on the shark dive, however only under the strict guidance of the assigned operator and after paying the "shark levy". The levy was doubled to F$ 10 per diver per day.

During 2004 the dive site was fully developed under the guidance of the Department of Fisheries. This included purchasing and setting of moorings, buoys, and signposts as well as the development of liability waivers and defining of safety procedures. Training of local fish wardens from the island of Beqa and Yanuca and the villages of Wainiyabia and Galoa in cooperation with the Department of Fisheries was initiated. A dedicated boat for the fish wardens was purchased and a steering committee was established in order to ensure the long-term management of the marine park.

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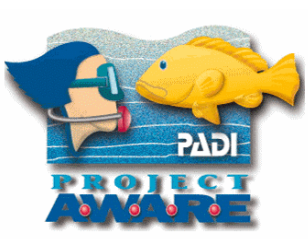

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